# THE IMPACT OF PLANKTIVORY ON THE LIFE HISTORIES OF ESTUARINE CRABS

by
Steven Gaines Morgan
III



Thesis submitted to the Faculty of the Graduate School
of the University of Maryland in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
1986

APPROVAL SHEET

Title of Thesis: The Impact of Planktivory on the Life Histories of Estuarine Crabs

Name of Candidate: Steven G. Morgan
Doctor of Philosophy, 1986

Dissertation and Abstract Approved: Marjorie L. Reaka

Marjorie L. Reaka
Associate Professor
Department of Zoology

Date Approved: November 25, 1986

ABSTRACT

Title of thesis: The impact of planktivory on the life history patterns of estuarine crabs

Name of candidate: Steven G. Morgan, Doctor of Philosophy, 1986

Thesis directed by: Dr. Marjorie L. Reaka, Associate Professor, Zoology

Estuarine crabs commonly display two larval dispersal patterns in which larvae are either exported from or retained within estuaries. Explanations for the disparate dispersal patterns are that larvae differ in their susceptibility to predation, which is greater within the estuary than offshore, or in their physiological tolerances to the large temperature and salinity fluctuations of the estuary.

Crab larvae which are exported from the estuary survived better in stressful temperature and salinity combinations than those which are retained, and thus the physiological stress hypothesis was rejected. However, exported larvae were more vulnerable to predation by fishes and invertebrates than were retained larvae. The long spines, large body sizes and behavioral responses of retained crab larvae were more effective at deterring predation by two fishes and eleven invertebrates in the laboratory, than were the short spines and small body sizes of exported larvae.

Spines generally were more effective against planktivorous fishes than against invertebrates. Spines operated

by effectively increasing the size of the larvae and their unpalatability to fishes. Behavioral observations revealed that fishes repeatedly attacked zoeae, but would quickly learn to avoid the noxious prey. The armor of crab larvae enabled them to survive attacks, and fishes repeatedly attempting to swallow long-spined crab larvae frequently would die. Spines did not assist in the flotation or stabilization of crab larvae.

Electivities of the three predominant fishes sampled from the Newport River estuary, North Carolina, also were greater for exported than retained species of crab larvae. Predation by larval and juvenile fishes was greater upstream compared to downstream, and greater diurnally than nocturnally. By hatching on nocturnal high tides, larvae rapidly disperse downstream where the probability of predation diminishes. Semiterrestrial crabs hatch on nocturnal spring tides to prevent stranding in tidal creeks. Thus, the hatching rhythms and dispersal patterns of crabs appear to have evolved in concert to transport larvae into coastal waters where the risk of predation is reduced, or to retain larvae within estuaries depending upon the vulnerability of the larva to predation.

ACKNOWLEDGMENTS

I am grateful to Marjorie Reaka for her support during my tenure at the University of Maryland. I thank Brian Feifarek for assistance with the field studies, Bryan Milstead for helping with data analysis, and Estelle Russek for providing statistical advice. Helpful suggestions were provided by David Allan, Thomas Cronin, Anson Hines, Clay Pierce, Michael Salmon, and Geerat Vermeij. John Costlow and Daniel Ritschoff made available the facilities of the Duke University Marine Laboratory, and Donald Hoss and Allan Powell offered access to the facilities of the National Marine Fisheries Service Laboratories in Beaufort, North Carolina. Funding was provided by the Chesapeake Bay Foundation and Sigma Xi. Finally, I am grateful to my parents for their moral and financial support.

TABLE OF CONTENTS

# LIST OF TABLES

# LIST OF FIGURES

# PREFACE

Estuarine crabs display two basic dispersal patterns whereby zoeae are either retained within or exported from estuaries. Selection could favor export of larvae from estuaries if survival or growth is greater outside than inside the estuary. Differential tolerances of zoeae to large fluctuations in temperature and salinity, or differential vulnerability to predation, may have selected for these disparate dispersal patterns if coastal waters are more stable or contain fewer predators than estuaries.

In Chapter One, the physiological stress hypothesis was tested by subjecting larvae of two species of crabs that inhabit the upper estuary to stressful temperatures and salinities in the laboratory. Larvae which are exported from the estuary should be less tolerant of low salinities and high temperatures than zoeae which are retained in the estuary.

The remainder of the dissertation is devoted to examining the effect of planktivory on the reproductive and larval biology of crabs. In Chapter Two, feeding trials and behavioral observations were conducted in the laboratory to determine if crab zoeae possess effective morphological and behavioral antipredatory adaptations against fish and invertebrate predation, and to describe their mode of operation. The antipredatory adaptations of freshwater zooplankters were compared to those of crab larvae.

In Chapter Three, the morphological and behavioral adaptations of six estuarine decapod zoeae to fish predation were examined in the laboratory to determine if zoeae exported to coastal waters are more susceptible to fish predation than zoeae which are retained in the estuary throughout development. In Chapter Four, electivities of fishes for five species of decapod zoeae in the Newport River estuary, North Carolina were determined at an upstream and downstream site, on spring and neap tides, and nocturnally and diurnally. If fish predation on zoeae is predictable in time and space, then the life history patterns of crabs should have evolved to reduce the effects of planktivory.

In Chapter Five, the preferences of eleven invertebrate predators for zoeae which are exported from or retained within estuaries were determined to test the hypothesis that exported larvae are more likely to be preyed upon than retained larvae. A review of available literature on the distribution, abundance and food habits of estuarine and coastal invertebrates was conducted to determine if predation pressure on crab zoeae is greater in estuaries than in coastal waters.

# CHAPTER 1

## ADAPTIVE SIGNIFICANCE OF HATCHING RHYTHMS AND DISPERSAL PATTERNS OF ESTUARINE CRAB LARVAE: AVOIDANCE OF PHYSIOLOGICAL STRESS BY LARVAL EXPORT?

## ABSTRACT

Estuarine crabs commonly display two larval dispersal patterns in which larvae are either exported or retained within estuaries. The semiterrestrial fiddler crab, *U. minax*, hatches on nocturnal spring tides in the upper estuary and larvae are rapidly transported downstream. The mud crab, *Rhithropanopeus harrisii*, hatches on nocturnal high tides of any amplitude and larvae are retained behaviorally in the upper estuary throughout development. If larvae are exported from the estuary to avoid environmental stress, then exported larvae should be less tolerant of high temperatures and low salinities than retained larvae. Larvae of these two species of estuarine crabs were hatched at 20 °/oo and 25°C and subjected to salinities of 0, 5, 10, 15, 20 and 30 °/oo, temperatures of 25 and 35°C, and exposure times of 2, 6, 12, and 48 h. Larvae of both species reared at 20 and 30 °/oo survived well, and those reared in deionized water all died within two hours regardless of temperature. Mud crab larvae survived better at the lower temperature (25 °C), the higher salinity (10 °/oo), and shorter exposure times. There was no significant effect of salinity or exposure time on the survival of fiddler crab larvae reared at the lower temperature, and survival decreased with increasing exposure time at the higher temperature. Thus the hypothesis that fiddler crab larvae are exported into stable coastal waters to reduce physiological stress is

not supported. However, the greater temperature and salinity tolerances of fiddler crab larvae suggests that synchronous hatching on spring tides by semiterrestrial crabs may have evolved to facilitate dispersal from tidal creeks where environmental conditions are least conducive to larval survival.

# INTRODUCTION

Most marine organisms have a complex life cycle in which the larval phase disperses from the adult habitat to develop in the plankton before returning to the habitat and metamorphosing. Organisms inhabiting estuaries along the east coast of the United States commonly display two larval dispersal patterns in which larvae are either exported or retained within estuaries. Estuarine organisms that retain their larvae in estuaries include molluscs, barnacles, decapods and fishes (Bousfield, 1955; Wood and Hargis, 1971; Sandifer, 1975; Goy, 1976; Cronin, 1982; Ouellet and Dodson, 1985; Weinstein et al., 1980), whereas barnacle nauplii and decapod larvae are exported into coastal waters (Bousfield, 1955; Dudley and Judy, 1971; Sandifer, 1973; Christy and Stancyk, 1982; Truesdale and Andryszak, 1983).

Selection could favor export of larvae from estuaries if 1) spreading larvae over several estuaries damps variation in survival and reproduction of an individual's descendents (Strathmann, 1974), or 2) survival or growth of larvae is greater outside the estuary (Christy, 1982; Strathmann, 1982). Simulation models of the consequences of larval dispersal on different spatial scales and under different patterns of environmental variation revealed that there is no advantage to spreading larvae among estuaries when the carrying capacities or probabilities of invading an estuary differ consistently (Palmer and

Strathmann, 1981). Furthermore, adaptation to local conditions and homing by organisms provide indirect evidence against the hypothesis that spatial and temporal variability of estuaries has selected for dispersal of larvae among estuaries (Strathmann, 1982).

However, larvae may be exported from the estuary if starvation, predation or physiological stress reduces the probability of survival or growth in the estuary. Estuaries are generally at least as productive as coastal waters (Ryther, 1959; Malone, 1977; Ferguson et al., 1980), so that it is unlikely that larvae will find more food offshore. However, the greater productivity of estuaries does support more predators (Weinstein, 1979; Boesch and Turner, 1984), and therefore, predation may be less in coastal waters. Strathmann (1982) compiled the instantaneous mortality rates of copepods in estuarine and coastal waters and found that mortality rates were greater in estuaries.

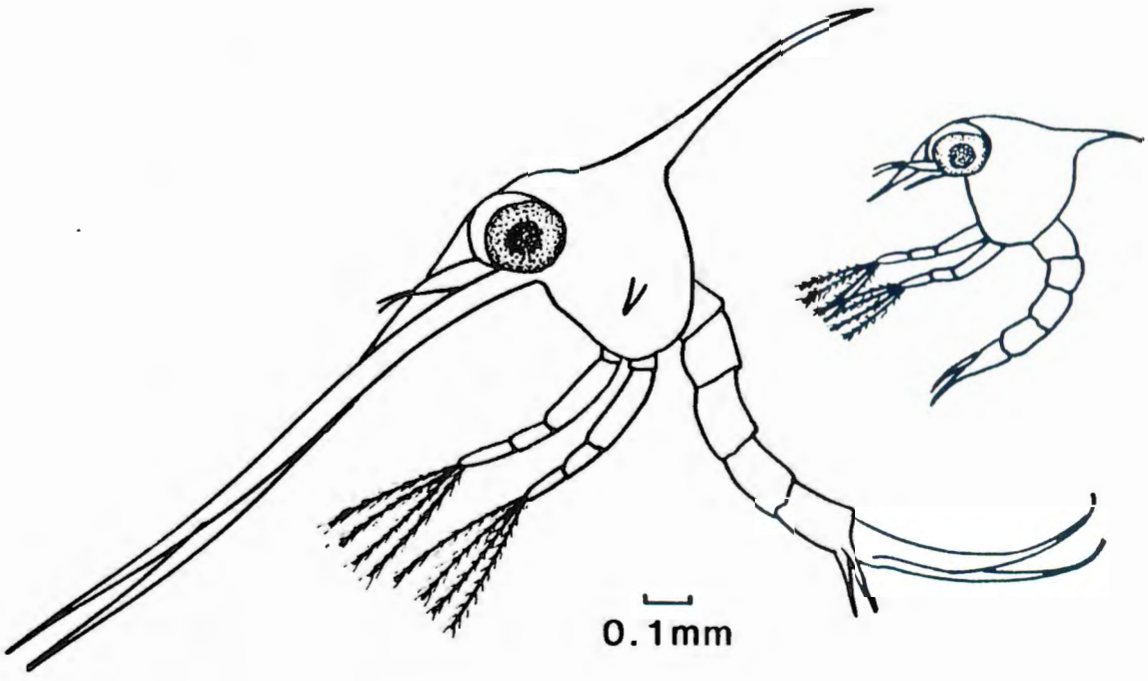
There is also evidence to support the hypothesis that larval export may have evolved to reduce physiological stress. Semiterrestrial crabs release their larvae into waters of shallow tidal creeks, which may have salinities of 0 °/oo and temperatures exceeding 40°C during the day (Dollard, 1980). At 40°C and 10°/oo, 50 % of newly-hatched larvae of the fiddler crabs, *Uca minax*, die in 1 h of exposure (Vernberg and Vernberg, 1975). Thus, semiterrestrial crabs hatch on nocturnal spring tides when

the water volume is greatest in the upper estuary, and consequently the larvae are swept rapidly downstream on ebbing spring tides, which minimizes their exposure to low salinities and high temperatures (Wheeler, 1978; Saigusa, 1981; Christy, 1982).

If newly hatched larvae are transported from the estuary to avoid environmental stress, then exported larvae should be less tolerant of high temperatures and low salinities than retained larvae. However, if the tolerances of exported larvae are greater than or equal to those of retained larvae, then larvae are not exported from the estuary to escape physiological stress.

To test these hypotheses, I selected two species of crabs which coexist at the heads of estuaries in salinities of 0-25 $^{o}/_{oo}$. Larvae of the semiterrestrial fiddler crab, *Uca minax* (Figure 1), hatch on nocturnal spring tides and are exported from the estuary (Christy and Stancyk, 1982; Truesdale and Andryszak, 1983; Salmon et al., 1986). In contrast, larvae of the subtidal mud crab, *Rhithropanopeus harrisii* (Figure 1), hatch within several hours of sunset on high tides of any amplitude (Forward, 1986). Furthermore, mud crabs have evolved behavioral mechanisms that enable them to remain in the upper estuary (Cronin, 1982; Lambert and Epifanio, 1983). The experiment was designed to determine the larval survival of both species following exposure to high temperatures and low salinities for various durations.

Figure 1. First instar A) R. harrisii and B) U. minax.


0.1mm

## METHODS AND MATERIALS

Ovigerous *U. minax* and *R. harrisii* were collected at low tide from the North and Neuse Rivers, North Carolina, respectively. Crabs were placed individually in 20 °/oo water contained in 19 cm culture dishes. All ovigerous females were maintained at 25 °C and at a photoperiod of 12 h light:12 h dark. Larvae from four hatches of each species were subjected to salinities of 0, 5, 10, and 15 °/oo, temperatures of 25 and 35 °C, and exposure times of 2 h, 6 h, 12 h and 48 h. These larvae were compared to those reared at more favorable salinities (20 °/oo for mud crab larvae and 20 and 30 °/oo for fiddler crab larvae). Seawater was diluted with distilled water and allowed to stand for at least one day prior to use in experiments. Larvae were introduced immediately after hatching into waters of appropriate temperature, but were allowed to acclimate for approximately 20 min at intermediate salinities if the change in salinity was greater than 10 °/oo. All larvae not being reared under constant temperatures and salinities were reintroduced to 20 °/oo seawater following their exposure to lower salinities. The same acclimation procedure was followed for larvae undergoing changes greater than 10 °/oo. Fifty larvae (10 larvae in each of five 4 cm culture dishes) were reared at each combination of temperature, salinity and exposure time. Larvae were fed *Artemia* nauplii and provided with clean water daily. Survival was monitored immediately

following the designated exposure time and 24 h and 48 h after the beginning of the experiment. The experiment was terminated after two days prior to the onset of molting to the second instar. Survival data were arcsine transformed, and orthogonal polynomial contrasts were analyzed by the analysis of variance.

## RESULTS

Both fiddler crab and mud crab larvae reared at control salinities (20, 30 °/oo) survived well (>95% survival), whereas all larvae died within two hours when reared in deionized water. Fiddler crab larvae survived significantly better at extreme temperatures and salinities than did mud crab larvae (Figure 2, Table 1). Significantly more first instar mud crab larvae survived at the lower temperature (25°C) and the higher salinity (10 °/oo) than at the higher temperature (35 °C) and lower salinity (5 °/oo). Mud crab larvae exposed to stressful temperatures and salinities survived better as exposure time decreased, except for those chronically exposed (48 h) to only one salinity. There was no significant effect of salinity or exposure time on the survival of fiddler crab larvae reared at 25°C, and larval survival only decreased with increasing exposure when reared at 35°C.

## DISCUSSION

Selection for export or retention of estuarine larvae does not appear to be due to differential temperature and

Figure 2. Percent survival of A) *U. minax* and B) *R. harrisii* zoeae reared under different combinations of temperature, salinity and exposure time.

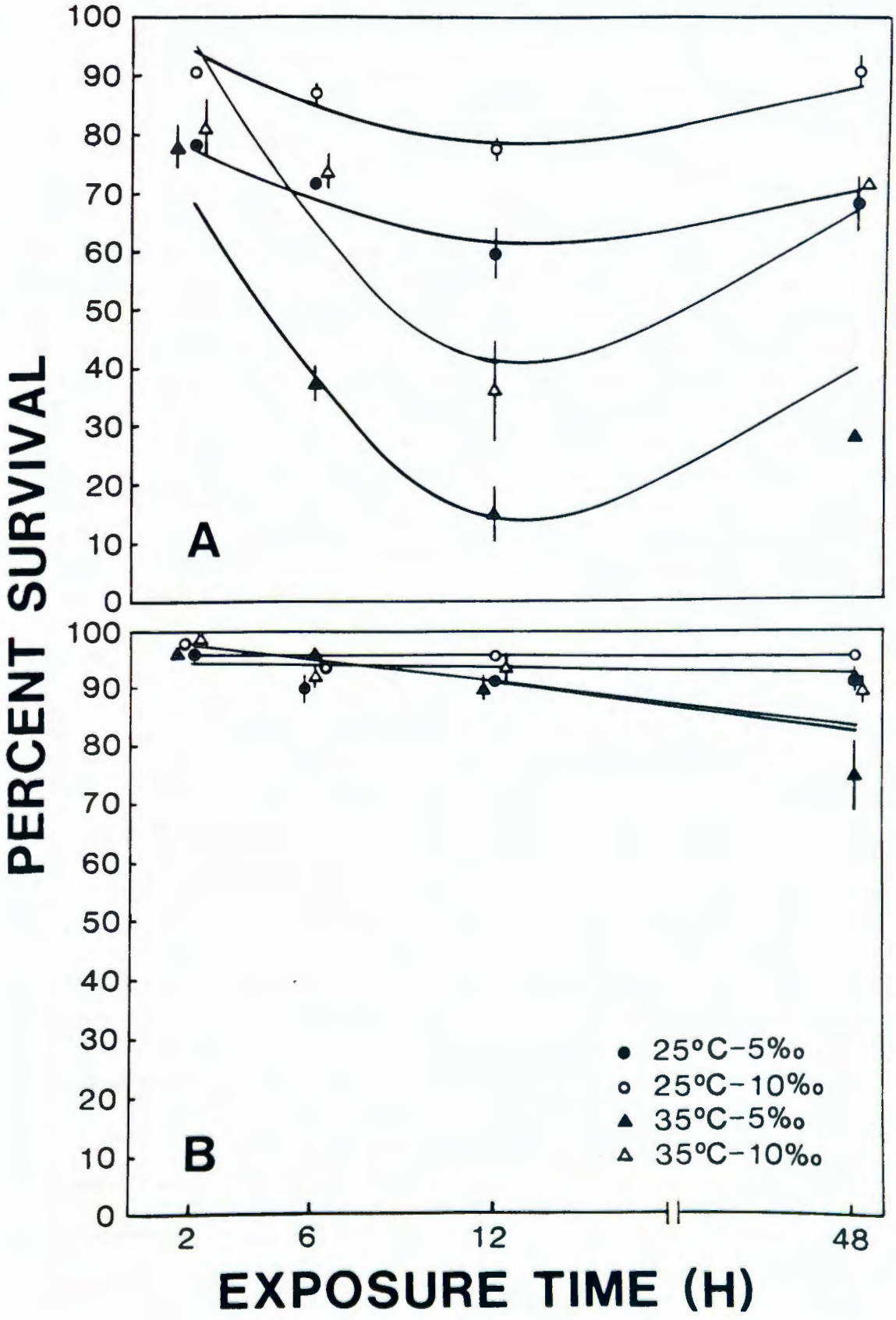

PERCENT SURVIVAL
100
90
80
70
60
50
40
30
20
10
0
A
B
25°C-5‰
25°C-10‰
35°C-5‰
35°C-10‰
2
6
12
48
EXPOSURE TIME (H)

Table 1. Results of three-way ANOVA of temperature, salinity and exposure effects on A) *R. harrisii* and B) *U. minax* larvae.

A. *Rhithropanopeus harrisii*

| Source | df | SS | F Value | P Value |
|---|---|---|---|---|
| Model | 6 | 4.5788 | 18.79 | .001 |
| Temperature | 1 | 1.4475 | 35.64 | .001 |
| Salinity | 1 | 1.1027 | 27.15 | .001 |
| Exposure | 1 | 1.1037 | 27.18 | .001 |
| Exposure$^2$ | 1 | 1.4087 | 34.69 | .001 |
| Temp x Exp | 1 | 0.4326 | 10.65 | .01 |
| Temp x Exp$^2$ | 1 | 0.3701 | 9.11 | .01 |
| Error | 56 | 1.9404 | | |
| Total | 62 | 6.8530 | | |

B. *Uca minax*

| Source | df | SS | F Value | P Value |
|---|---|---|---|---|
| Model | 4 | 0.2867 | 2.62 | .05 |
| Temperature | 1 | 0.0188 | 0.69 | NS |
| Salinity | 1 | 0.0743 | 2.72 | NS |
| Exposure | 1 | 0.1719 | 6.28 | .05 |
| Exposure$^2$ | 1 | 0.0210 | 0.77 | NS |
| Error | 59 | 1.6138 | | |
| Total | 63 | 1.901 | | |

salinity tolerances of the larvae. Although fiddler crab larvae are exported from the estuary, they can tolerate temperature and salinity extremes better than mud crab larvae, which are retained within the estuary. Fiddler crab larvae may have evolved a greater tolerance of extreme temperatures than mud crab larvae have because, unlike R. harrisii, *U. minax* often release their larvae into tidal creeks. *Uca minax* are more abundant along creeks than the river because they prefer substrates of higher organic content for feeding and perhaps burrow construction (Whiting and Moroshi, 1974). Fiddler crab larvae hatched in creeks may become stranded in pools as the tide ebbs, and suffer prolonged exposure to high temperatures and low salinities. To avoid stranding in tidal pools, fiddler crabs may hatch on nocturnal spring tides to facilitate dispersal into deeper channels where environmental conditions are generally less severe. Corks used to simulate larvae all accumulated in tidal pools when released at spring low tide, whereas they were carried out to sea on a spring high tide (Saigusa, 1981). Furthermore, Saigusa (1981) found that two species of *Sesarma* which are less tolerant of freshwater hatch in closer synchrony with the nocturnal spring tides than does a third species which is more tolerant.

Mud crab larvae may be less tolerant of physiological stress and hatch on nocturnal high tides of any amplitude, because they hatch subtidally and are much less likely to

become stranded in tidal pools. Furthermore, mud crab larvae can regulate their position in the estuary, so that they can avoid physiological stress and congregate in areas most conducive to their development (Cronin, 1982).

Mud crab larvae generally survived better in constant salinities than fluctuating salinities. Thus, change in salinity is apparently more stressful than prolonged exposure for mud crab larvae. However, fiddler crab larvae would be more able to withstand salinity fluctuations over a series of tidal cycles if stranded in a tidal pool unless they hatched in freshwater. Saigusa (1981) found that two species of Sesarma larvae hatched and reared in either spring water or tap water died within 48 h, and a third species died within 70 h. In the present study, fiddler and mud crab larvae that were hatched at higher salinities and introduced to freshwater after a brief acclimation period died within two hours. Thus, larvae acclimated to freshwater or low salinities may survive longer than those which are hatched at higher salinities and then are quickly swept into freshwaters.

Fiddler crab larvae may have evolved to be very tolerant of extreme temperature and salinity and hatch on nocturnal spring tides to facilitate survival in and dispersal from tidal creeks. However, semilunar hatching may also have evolved to rapidly disperse larvae from the estuary, not to avoid physiological stress but to escape predation. Young planktivorous fishes are most abundant

in low salinity waters where fiddler and mud crabs hatch (Cain and Dean, 1976; Crabtree and Dean, 1979; Weinstein, 1979; Hunter, 1980; Boesch and Turner, 1984). Peak hatching of fiddler crabs may occur on spring high tides to disperse the larvae quickly from tidal creeks and the upper estuary where predation could be greatest.

Mud crabs hatch subtidally and are retained in the upper estuary, so they hatch on any nocturnal high tide. In fact, Forward (1986) has determined that larval release occurs on high tides only when they occur between 2 h after sunset and 3-5 h before sunrise. When high tide occurs at other times, larvae are hatched soon after sunset regardless of the tidal phase. Therefore, hatching early in the evening is more important than hatching on high tide, and so reducing vulnerability to predators is probably more important than avoiding physiological stress or promoting initial seaward transport.

## LITERATURE CITED

Anderson, D. M. and K. D. Stolzenbach. 1985. Selective retention of two dinoflagellates in a well-mixed estuarine embayment: the importance of diel vertical migration and surface avoidance. Mar. Ecol. Progr. Ser. 25: 39-50.

Boesch, D. F. and R. E. Turner. 1984. Dependence of fishery species on salt marshes: the role of food and refuge. Estuaries 7: 460-468.

Bousfield, E. L. 1955. Ecological control of the occurrence of barnacles in the Miramichi estuary. Bull. Nat. Mus. Canada 137: 1-69.

Cain, R. L. and J. M. Dean. 1976. Annual occurrence, abundance and diversity of fish in a South Carolina intertidal creek. Mar. Biol. 36: 369-379.

Christy, J. H. 1982. Adaptive significance of semilunar cycles of larval release in fiddler crabs (Genus Uca): test of an hypothesis. Biol. Bull. 163: 251-263.

Christy, J. H. and S. E. Stancyk. 1982. Movement of larvae from North Inlet estuary, S. C., with special reference to crab zoeae. In: Estuarine Comparisons, V. Kennedy, Ed. Academic Press, New York.

Crabtree, R. E. and J. M. Dean. 1982. The structure of two South Carolina estuarine tide pool fish assemblages. Estuaries 5: 2-9.

Cronin, T. W. 1982. Estuarine retention of larvae of the

crab *Rhithropanopeus harrisii*. Estuar. Coast. Shelf Sci. 15: 207-220.

Dollard, H. A. 1980. Larval release patterns in the wharf crab, *Sesarma cinereum*, from North Inlet, South Carolina. Masters thesis, University of South Carolina, 34 p.

Dudley, D. L. and M. H. Judy. 1971. Occurrence of larval, juvenile, and mature crabs in the vicinity of Beaufort Inlet, North Carolina. NOAA Tech. Rep. NMFS SSRF-637, 10 pp.

Ferguson, R. L., G. W. Thayer and T. R. Rice. 1980. Marine primary producers. In: Functional Adaptations of Marine Organisms. J. Vernberg (ed.), Academic Press, NY, pp. 9-69.

Forward, R. B., Jr., J. K. Douglass and B. E. Kenney. 1986. Entrainment of the larval release rhythm of the crab Rhithropanopeus harrisii (Brachyura: Xanthidae) by cycles in salinity change. Mar. Biol. 90: 537-544.

Goy, J. W. 1976. Seasonal distribution and the retention of some decapod crustacean larvae within the Chesapeake bay, Virginia. Masters thesis, Old Dominion University, Norfolk, Virginia, Pp. 1-101.

Lambert, R. and C. E. Epifanio. 1983. Comparison of dispersal strategies in two genera of brachyuran crab in a secondary estuary. Estuaries 5: 182-188.

Malone, T. C. 1977. Plankton systematics and distribution. MESA New York Bight Atlas Monograph 13, New York Sea

Grant, Albany, 41 pp.

Ouellet, P. and J. J. Dodson. 1985. Dispersion and retention of anadromous rainbow smelt (Osmerus mordax) larvae in the middle estuary of the St. Lawrence River. Can. J. fish. Aquat. Sci. 42 332-341.

Palmer, A. R. and R. R. Strathmann. 1981. Scale of dispersal in varying environments and its implications for life histories of marine invertebrates. Oecologia 48: 308-318.

Ryther, J. H. 1959. Potential productivity of the sea. Science 130: 602-608.

Saigusa, M. 1981. Adaptive significance of semilunar rhythm in the terrestrial crab *Sesarma*. Biol. Bull. 160: 311-321.

Salmon, M., W. H. Seiple and S. G. Morgan. 1986. Hatching rhythms of fiddler crabs and associated species at Beaufort, North Carolina. J. Crust. Biol. 6: 24-37.

Sandifer, P. A. 1973. Distribution and abundance of decapod crustacean larvae in the York River Estuary and adjacent lower Chesapeake Bay, Virginia, 1968-1969. Chesapeake Sci. 14: 235-257.

Strathmann, R. R. 1974. The spread of sibling larvae of sedentary marine invertebrates. Amer. Natural. 108 (959): 29-44.

Strathmann, R. R. 1982. Selection for retention or export of larvae in estuaries. In: Estuarine Comparisons. V. Kennedy, Ed. Academic Press, Inc., NY, p. 521-536.

Thayer, G. W., D. E. Hoss, M. A. Kjelson, W. F. Hettler, Jr. and M. W. Lacroix. 1974. Biomass of zooplankton in the Newport River estuary and the influence of postlarval fishes. Chesapeake Sci. 15: 6-19.

Truesdale, F. M. and B. L. Andryszak. 1983. Occurrence and distribution of reptant decapod crustacean larvae in neritic Louisiana waters: July 1976. Contr. Mar. Sci. 26: 37-53.

Vernberg, F. J. and W. b. Vernberg. 1975. Adaptations to extreme environments. In: Physiological ecology of estuarine organisms. F. J. Vernberg, Ed. University of South Carolina Press, Columbia, 165-180 p.

Weinstein, M. P. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. Fish. Bull. 77: 339-357.

Weinstein, M. P., S. L. Weiss, R. G. Hodson and L. R. Gerry. 1980. Retention of three taxa of postlarval fishes in an intensively flushed tidal estuary, Cape Fear river, North Carolina. Fish. Bull. 78(2): 419-436.

Wheeler, D. 1978. Semi-lunar hatching periodicity in the mud fiddler crab *Uca pugnax* (Smith). Estuaries 1: 268-269.

Whiting, N. H. and G. A. Moroshi, 1974. Certain organism-substrate relationships affecting the distribution of *Uca minax* (Crustacea): Decapoda). Hydrobiologia 44(4): 481-493.

Wood, L. and W. J. Hargis, Jr. 1971. Transport of bivalve larvae in a tidal estuary. In: Proceedings of the Fourth European Marine Biology Symposium. D. J. Crisp, Ed. Cambridge University Press, Cambridge, 29-44 p.

# CHAPTER 2

## ADAPTIVE SIGNIFICANCE OF SPINATION IN ESTUARINE CRAB ZOEAE

## ABSTRACT

The adaptive significance and mode of operation of the spines of mud crab, Rhithropanopeus harrisii, zoeae were investigated. Spines did not appear to assist in the flotation of R. harrisii zoeae, because the settling velocity of spined zoeae versus zoeae with their spines removed did not differ significantly. Rhithropanopeus harrisii zoeae are capable of flaring their antennal spines perpendicularly to their body which does retard their sinking rate, but zoeae do not flare their spines unless molested. Spines are not needed to stabilize the zoeae because zoeae assume their normal orientation following spine amputation, and sinking zoeae do not oscillate regardless of whether spines are present or not. Although despined R. harrisii zoeae were preferred over spined zoeae by only one of ten planktonic and benthic invertebrate predators in laboratory feeding trials, spines limited the size at which small benthic-feeding and planktivorous fishes began preying on zoeae. Both Menidia menidia and Fundulus heteroclitus were able to consume more despined than spined R. harrisii zoeae. Long-spined R. harrisii zoeae that were attacked by M. menidia had the same survival and duration to metamorphosis as did zoeae that were not attacked. More Sesarma reticulatum, which has shorter spines than R. harrisii, died following attacks by silversides than did zoeae that were not attacked. The long spines of R. harrisii sometimes broke during fish attacks but the body

remained intact, whereas S. reticulatum zoeae frequently were mangled following attacks. Partially regenerated spines were as effective as unbroken spines at deterring predation by M. menidia.

Spines operated by effectively increasing the size of the zoeae, and could be more effective than a large body at preventing predation. Spined, first instar R. harrisii zoeae were at least as effective as despined second and third instar (but not fourth instar) zoeae at withstanding predation by M. menidia. The noxious qualities of spines make them more effective than an increase in body size. All twelve 16 mm M. menidia fed only R. harrisii zoeae died within eight days, whereas fish fed despined R. harrisii, Artemia nauplii, S. reticulatum zoeae, or nothing survived. Autopsies revealed that zoeae often were lodged in the pharynx of silversides. Fundulus heteroclitus preyed on R. harrisii zoeae at a smaller size than did M. menidia, and did not die when fed a steady diet of zoeae, indicating that large-mouthed demersal fishes are better able to handle armored prey. Behavioral observations of first and fourth instar R. harrisii zoeae indicated that spined zoeae were avoided more by fish than were despined zoeae, whereas despined zoeae were captured, mouthed and ingested more than spined zoeae. Thus small fishes appeared to be able to distinguish spined from despined zoeae and quickly learned to avoid spined zoeae. Rhithropanopeus harrisii zoeae did not attempt to evade fish attacks, but instead relied on

their armor and postcontact behavioral defenses.

# INTRODUCTION

Planktonic organisms possess an array of possible morphological, chemical or behavioral antipredatory adaptations (Zaret and Suffern, 1976; Kerfoot, 1977a; Drenner et al., 1978; Cowden et al., 1984). Although occasional observations have been recoreded of defense mechanisms in marine larvae, the effectiveness of the alleged antipredatory adaptations rarely has been documented experimentally. To demonstrate that a trait could have evolved in response to predation, one must, 1) examine sympatric predators and prey, 2) show that the trait increases the fitness of the prey, and 3) investigate other possible functions of the character to determine if it could have evolved for more than one purpose (Williams, 1966; Gould and Lewontin, 1979; Vermeij, 1982). The effectiveness of the antipredatory device may differ among predators using different modes of feeding, so a variety of common predators should be employed to test the relative effectiveness of the trait. The encounter frequency, the severity of the interaction, and the ability of the predator and prey to learn to avoid or diminish the consequences of the encounter all may determine the rate of evolution of the character.

Spines have been shown to serve an antipredatory function in freshwater plankton communities by deterring copepod predation on rotifers (Gilbert, 1967) and cladocerans (Kerfoot, 1977a; O'Brien et al., 1979). Although spination is a particularly prominent characteristic of many

marine planktonic organisms, including algae, dinoflagellates, radiolarians, cladocerans, rotifers, trochophores, barnacle nauplii, stomatopod larvae, and decapod zoeae, experimental evidence on the effectiveness and mode of operation of this alleged antipredatory adaptation (Lebour, 1919; Hardy, 1956) of marine plankters is very limited.

Considering all plankters, freshwater and marine, spination is perhaps best developed among brachyuran zoeae. Crab zoeae are typically armed with rostral, antennal, dorsal, abdominal, and telson spines, some of which may be longer than the length of the larva. Thus, spines may effectively increase the size of the zoea in all directions without greatly increasing its visibility (O'Brien et al., 1979), which might be most effective against selective-feeding fishes, and especially larval fishes. A small increase in prey size will greatly decrease the profitability of the prey to a small fish, but will increase the handling costs to large fish only slightly (Werner, 1974).

Successful captures of prey depend on the previous experience of the fish and the prey type (Ware, 1972; Confer and Blades, 1975; Vinyard, 1980; Werner et al., 1981). Fish have been shown to learn to avoid spined sticklebacks (Hoogland et al., 1957) and distasteful insects (Kerfoot et al., 1980; Bronmark et al., 1984). If fishes can detect spines, and retain and utilize information concerning prior encounters with different types of prey, then they may be able to learn to avoid spined prey. Adult fishes can detect

spines, because they have been observed to nip off the extremely elongate spines of porcellanid zoeae in the field before ingesting the zoea (S. Stancyk, pers. comm.). However, larval fishes may not be able to detect spines because their visual acuity is poorer than that of adults (Durbin, 1979; Li et al., 1980; Hairston and Easter, 1982; Breck and Gitter, 1983; Unger and Lewis, 1983; Neave, 1984).

Although the discriminatory and learning capabilities of fish larvae are poorly known, the fish are apparently capable of actively selecting their prey in the field (Checkley, 1982; Peterson and Ausubel, 1984; Govoni et al., 1986), and appear to avoid crab zoeae. Alvarino (1980) surveyed the coastal waters of California for three years and discovered that the abundance of anchovy larvae was positively correlated with patches of zooplankton containing their prey (copepods, euphausiids), but was negatively correlated with patches containing crab zoeae. Furthermore, menhaden, herring and redfish larvae did not feed on crab zoeae even though the zoeae often were very abundant and similar in size to their prey (Mulkana, 1966; Marak, 1974; Hunter, 1980). Therefore, spines also may have noxious properites.

Spines must increase the probability of survival of the prey if the trait is to be selected for. Prey that survive attacks may suffer broken spines (Kerfoot, 1977a; Murtaugh, 1981; Vermeij, 1982). Dorsal spines of the mud crab,

Rhithropanopeus harrisii, are completely regenerated in two molts, and the antennal spines are incompletely regenerated within three molts (Freeman, 1983). Meanwhile, partially regenerated spines may continue to deter predation.

Spines of marine larvae appear to be more effective at deterring fish rather than invertebrate predators. The setae of trochophores did not significantly deter predation by a ctenophore, hydrozoan medusa, or brachyuran megalopa when compared to predation on presetose trochophores (Pennington and Chia, 1984). Nor did the setae of trochophores or the frontal horns of barnacle nauplii deter predation by filter feeding mussels and tunicates (Cowden et al., 1984). Furthermore, ctenophores have been reported to coexist with high densities of crab zoeae while the copepod population was being decimated (Cronin, 1962; Burrel and van Engel, 1976), indicating that ctenophores do not exert a strong impact on larval populations. Spines of planktonic organisms long have been hypothesized to serve as antipredator devices, but they also may have evolved to stabilize (Weldon, 1889) or to retard sinking (Hardy, 1956; Hutchinson, 1967) of the organism. Fisher (1977) has suggested that spines may inhibit lateral oscillations by the Pennsylvanian horseshoe crab, Euproops danae, following attack by vertebrate predators. Passively sinking organisms create fewer pressure waves and hence, the number of attacks incurred may be reduced.

Thus, elaborate armature is a pervasive characteristic

of marine planktonic organisms, but the adaptive significance of spines has yet to be demonstrated. Spines may have evolved to 1) decrease the energetic expenditure of plankters by assisting in the flotation of the organism, 2) reduce predation by stabilizing passively falling organisms so that fewer attacks are elicited, or 3) physically deter predation by small fishes or invertebrates. It is not sufficient to merely distinguish which of the various hypotheses could explain the evolution of armature; rather one also must determine the mechanism of operation and the degree of effectiveness of the trait.

Therefore, the objectives of the present paper also are to determine the ability of spines of crab zoeae to 1) deter predation by ten invertebrates as well as larvae and juveniles of two fishes; 2) to increase the fitness of the zoeae by a) deterring predation, b) increasing the survival and decreasing the development time of zoeae attacked by fish, and c) deterring fish predation even when regenerating broken spines; 3) to decrease the fitness of the predator due to noxious qualities; 4) to effectively increase the size of the zoeae; 5) to deter fish predation better than a large body. The ability of larval fish to detect long zoeal spines and to quickly learn to avoid prey bearing noxious spines also will be determined. Finally, selection for spines of marine and freshwater zooplankters will be discussed.

# METHODS AND MATERIALS

## Selection of Experimental Organisms

Mud crab, Rhithropanopeus harrisii, zoeae (Figure 1) were fed to two fish predators: the Atlantic silverside, Menidia menidia, and the killifish, Fundulus heteroclitus, and ten common and widely distributed invertebrates (Table 1). Mud crabs hatch from April to October in the Newport and Neuse River estuaries, North Carolina, and the zoeae are found primarily in the upper estuary in waters ranging from 0-25 o/oo. Silversides are selective diurnal planktivores occurring primarily in open waters, ranging from 0-36 o/oo (Bayliff, 1950). The killifish feeds opportunistically on a variety of prey, including armored prey (Kneib and Stiven, 1978), and also ranges throughout the estuary (Weinstein, 1979). Thus, both of these wide-ranging predators should encounter R. harrisii zoeae. Furthermore, the breeding season of the fishes is concurrent with that of the crabs (Kneib and Stiven, 1978; Middaugh, 1981), so that zoeae would be subject to larval fish predation.

## General Methodology

Gravid R. harrisii were collected from the Neuse River estuary, North Carolina, by using traps which lure crabs into oyster shells provided within. Gravid F. heteroclitus were collected with a 15 ft seine in tidal creeks at low tide. Gravid M. menidia were collected with a 50 ft seine in high salinity marshes at low tide in the Newport River estuary. All invertebrate predators were collected by hand

Figure 1. First instar zoeae of A) R. harrisii and B) S. [illegible].

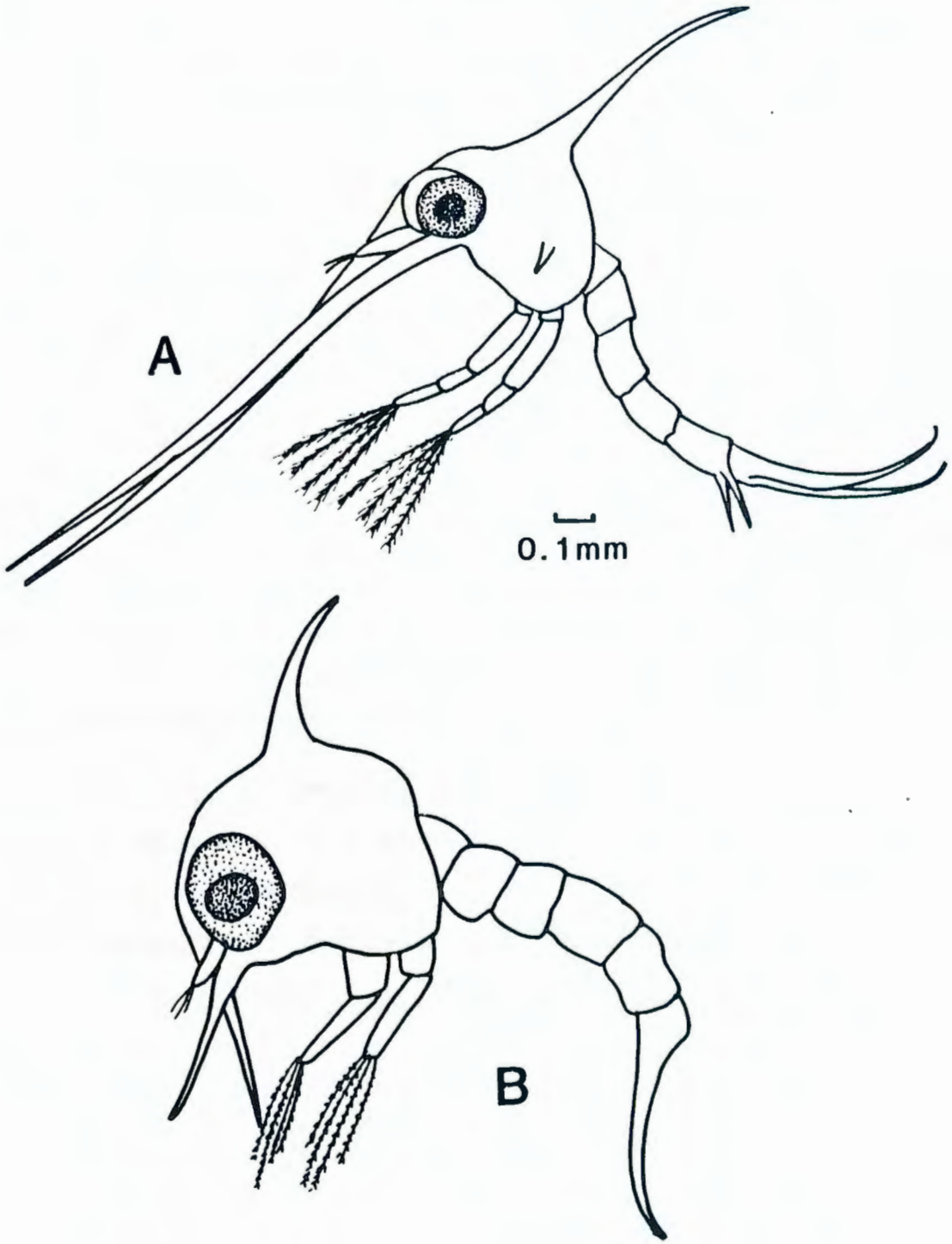


Table 1. Mean size and minimum and maximum size (mm) of 10 planktonic and benthic invertebrate predators, diameter of culture dishes (cm) used for feeding trials, number of crab larvae fed of each species, and number of replicates. Measurements (M.): L=length, W=width, H=height, BW=base width, and TW=distance from tip of tentacle to opposing tentacle tip.

| PREDATOR | TAXON/ COMMON NAME | PREDATOR SIZE M. | MEAN | MIN.-MAX. | DISH SIZE | NO. LARVAE | n |
|---|---|---|---|---|---|---|---|
| PLANKTONIC | | | | | | | |
| *Sagitta hispida* | Chaetognath | L: | 7.5 | 7-8 | 6 | 10 | 19 |
| *Eutima mira* | Hydromedusa | W: | 5.2 | 5-8 | 6 | 10 | 15 |
| *Mnemiopsis leidyi* | Ctenophore | L: | 23.5 | 17-30 | 9,19 | 20 | 8 |
| BENTHIC | | | | | | | |
| *Styela plicata* | Tunicate | H: | 43.3 | 31-67 | 19 | 25 | 10 |
| | | W: | 23.1 | 21-26 | | | |
| *Aiptasia pallida* | Anemone | BW: | 8.1 | 13-35 | 9 | 25 | 10 |
| | | TW: | 20.5 | 13-35 | | | |
| *Balanus amphitrite* | Barnacle | BW: | 12.7 | 10.0-16.0 | 6 | 20 | 14 |
| | | H: | 8.0 | 7.2-11.4 | | | |
| *Caprella penantis* | Amphipod | L: | 5.1 | 3-8 | 6 | 20 | 18 |
| *Palaemonetes pugio* | Grass shrimp | L: | 27.2 | 22.0-30.0 | 9 | 40 | 20 |
| *Rhithropanopeus harrisii* | Crab | W: | 9.6 | 8.7-10.8 | 9 | 40 | 20 |
| *Geukensia demissa* | Mussel | L: | 56.0 | 48-75 | 9 | 40 | 10 |

from the Newport River estuary.

Eggs of crabs and fishes were hatched in the laboratory and reared under a 12 h light: 12 h dark photoperiod. Crabs were hatched at 25oC and 25 o/oo. Fishes were hatched at ambient temperatures and salinities in flowing seawater (approximately 25oC and 28-33 o/oo. The naive predators and prey were used only once during experiments. Larvae were reared on Artermia nauplii. Predators were starved one day prior to experimentation, and fish were fed several drops of Artemia nauplii following the conclusion of the feeding trial to determine if they were still hungry. Only actively swimming zoeae displaying normal behavior were used in experiments.

Specific Methodology and Experimental Design

Rostral, antennal and dorsal spines of first instar R. harrisii were amputated with a scalpel under a dissecting microscope to determine the effectiveness of spines at deterring predation. Two basic experimental designs were employed in the spine removal experiments. In the first, either 12 despined or 12 spined R. harrisii were fed to a fish in a 6 cm bowl. On the following day, the same fish were fed 12 of the opposite typed of zoeae. Half of the ten fish were fed despined zoeae the first day, and the other half were fed spined zoeae first. The number of zoeae remaining after 24 h was recorded for each experiment.

In the second type of experiment, 12 despined and 12 spined zoeae simultaneously were fed to a fish in a 6 cm

bowl to offer the fish a direct choice for 24 h. Ten replicates for each size class of fish were also performed during the second experiment. A comparison of the results of each type of experiment was designed to reveal if the presence of spined zoeae affects predation on despined zoeae. If the co-occurrence of spined and despined zoeae results in fewer despined zoeae being consumed while the number of spined zoeae eaten remains unchanged, then feeding is being inhibited because fish cannot distinguish between prey. If fish can distinguish between spined and despined zoeae then despined zoeae should be preyed upon in greater numbers when fed the prey simultaneously rather than separately. If fish feed on similar numbers of spined and despined zoeae regardless of whether or not they were fed the zoeae separately or concurrently, then fish are probably unable to discriminate between the two prey types.

Two types of controls were employed to determine the effects of spine amputation on the survival of R. harrisii zoeae. In one type of control, despined and spined zoeae were placed either separately or together in bowls without fish predators to determine if significant differences in survival after 24 h occurred. A total of 30 replicates were performed using ten replicates from three different hatches.

In the second type of control, a sham operation was performed by amputating an antennule. These zoeae were fed separately and together with spined zoeae which had not undergone an operation to 14 mm silversides. Ten replicates

were performed with one hatch of larvae. Only freshly hatched zoeae were used for both control experiments because the first instar is the most sensitive to stress.

To determine if spines physically prevent predation by small fish (even when starved), despined and spined R. harrisii zoeae were fed to silversides ranging in size from 6-20 mm SL in 2 mm size class intervals. All four instars were used to determine the effectiveness of spine length at preventing fish predation as zoeae increased in size. Silversides were fed spined and despined zoeae separately and together for all four instars. In addition, first instar spined and despined zoeae fed together were offered to killifish 6, 8, and 10 mm long.

Behavioral observations on predator-prey interactions also were conducted during the first 10 min of feeding trials. Silversides were observed when fed first and fourth instar despined and spined zoeae separately and together. Killifish were observed only when fed first instar despined and spined zoeae concurrently. The change in behavior of predator and prey was determined by comparing the frequency of behaviors in the first five minutes with those in the second five minutes. The behavior of the fish was quantified using the following categories: avoidances, attacks, captures, ingestion, and unusual behavior following capture, such as shuddering, loss of upright orientation, sinking, and mouthing and shaking the zoea. Similarly, zoeal behavior was categorized as evasion or spine-flaring

after an encounter, or escape or spine-flaring after an attack. Prey were not replaced during the observation period, so behaviors were expressed as percentages to provide a comparison between prey of differing vulnerability at the two time intervals. Thus, avoidances and attacks were expressed as a percentage of the number of pursuits made by the fish. Similarly, the ratio of captures and escapes to attacks, and ingestions and unusual behaviors to captures were calculated.

The effectiveness of spine length versus body size at deterring predation also was determined more directly by feeding despined second stage R. harrisii zoeae with spined first instar zoeae to silversides capable of feeding on both types of zoeae. The experiment was repeated using despined third and fourth stage zoeae instead of second stage zoeae. Despined and spined zoeae were fed to fish either separately or concurrently.

The effectiveness of regenerated spines (as compared to normal ones) at preventing predation was determined by amputating spines of second instar zoeae and rearing them to the third or fourth instar to enable spines to regenerate. The partially regenerated spines of the third instar were shorter than the regenerating spines of fourth instar zoeae. Zoeae with partially regenerated spines were then fed to silversides together with zoeae of the same hatch that had not been operated upon. Second instar zoeae were operated upon rather than first instar zoeae, because first

instar zoeae are more sensitive than second instar zoeae.

To determine if spine length is associated with increased survival and decreased larval development time for zoeae attacked by fish, R. harrisii, bearing long spines on a moderately sized body, and S. reticlatum (Figure 1), bearing short spines on a large body, were fed separately to 18 mm silversides. The total size (spine length plus body size) of each species is comparable and should have presented the fish with prey of similar difficulty. The silversides were capable of ingesting both prey, but only with some difficulty. Therefore, most zoeae were removed with a pipet for rearing following initial attacks and prior to ingestion.

Larval survival and duration to megalopa were determined for 360 freshly hatched zoeae (120 from each of three hatches) of each species that had not been attacked by silversides, and compared to 360 that had. Fifty larvae which were taken from the three hatches of each species but were not introduced to fish also were reared. The incidence of spine breakage of all zoeae was recorded on the second day of the experiment.

To determine if long spines possess noxious qualities that can induce mortality of the predator, silversides and killifish were fed 100 spined R. harrisii (long spines and small body size), 100 despined R. harrisii, 100 S. reticulatum (short spines and large body size), Artemia nauplii, or nothing for eight days. Twelve replicates each were

performed in 6 cm bowls for 18 mm silversides and 6 mm and 18 mm killifish. Five replicates were done for 40 mm silversides placed in 10 l containers, but the despined R. harrisii and S. reticulatum treatments were not performed. The number of fish surviving was monitored daily. Autopsies were performed on 18 mm silversides that died during the experiment.

Invertebrate predators were placed in culture dishes and were allowed to adjust to laboratory conditions for at least one day prior to experimentation. The size of the culture dishes used in the feeding trials and the number of larvae fed in a single trial depended upon the size of the predators (Table 1). Despined and spined zoeae were fed to the invertebrate predators separately as described above for the fish predation experiments.

The settling velocity of first instar R. harrisii zoeae with their spines amputated, flared or collapsed in the normal resting position was measured after placing them in a 45.7 X 6 X 7.5 cm plexiglass column. Zoeae descended 15.2 cm to allow them to attain maximum settling velocity, which then was measured over the next 30.5 cm. All zoeae were killed by placing them for one minute under a hot light, which caused many zoeae to flare their spines.

## RESULTS

### Experimental Controls

Both types of controls indicated that spine amputation did not significantly affect the survival of R. harrisii

zoeae. Survival was not significantly different between spined and despined zoeae regardless of whether they were placed in bowls separately or together (df=3,44; F=0.59; p=0.627). Nor was survival of zoeae that had an antennule removed significantly different from those that were not operated upon and fed to 14 mm silversides (df=1,26; F=0.03; p=0.862). In addition, all fish quickly consumed Artemia nauplii which were offered at the conclusion of each feeding trial, indicating that fish were still hungry even though zoeae usually remained.

Spines Physically Prevent Predation by Small Fishes

Significantly more R. harrisii zoeae which had their spines surgically removed were preyed upon by smaller size classes of fishes than were zoeae that were not operated upon (Figure 2, Table 2). Silversides 6 mm long were not capable of feeding on either despined or spined first instar zoeae, but 12 mm fish were able to consume all despined zoeae presented while feeding on only several spined zoeae. Nearly all spined zoeae were consumed by 16 mm fish.
A similar pattern resulted from feeding second instar R. harrisii zoeae to slightly larger fish, but the effectiveness of spines decreased. Silversides 8 mm long were incapable of feeding on either despined or spined second instar zoeae, but fish 14 mm long could consume all despined zoeae while preying on as many as seven spined zoeae. As was the case when first instar zoeae were fed to silversides, nearly all second instar spined zoeae were eaten by fish 8 mm

longer (18 mm) than those that were incapable of feeding on spined zoeae (10 mm fish). The effectiveness of spines to deter fish predation continued to decrease when third and fourth instar zoeae were fed to silversides. Fish 10 and 12 mm long were ineffective at preying on despined third or fourth instar zoeae, but fish 16-18 mm long (6 mm longer) would leave as many as seven or eight despined zoeae in contrast to five or ten spined zoeae, respectively.

Behavioral observations on first and fourth instar despined and spined R. harrisii zoeae indicated that spined zoeae were avoided more than despined zoeae, whereas despined zoeae were captured, mouthed, and ingested more than spined zoeae (Figure 3, 4; Table 3, 4). First instar despined zoeae were attacked and shaken more than spined zoeae, but not fourth instar despined zoeae. Fish feeding on spined zoeae occasionally shuddered, lost their upright orientation and sank motionlessly to the bottom of the dish with their mouths locked open. Silversides often shuddered violently several times before zoeae were dislodged from their mouths. Zoeae rarely darted away prior to an attack, but did so with slightly greater frequency after attack. Despined zoeae of either instar did not try to evade or escape significantly more than spined zoeae.

Small fish avoided spined and despined zoeae less often than did large fish, whereas the number of captures, mouthings, ingestions, and shakings was greater for larger fish (Figure 3, 4; Table 3, 4). The number of attacks,

Figure 2. Number of first to fourth instar (A-D) despined and spined *R. harrisii* zoeae remaining after 24 h when fed to *M. menidia* separately or together.

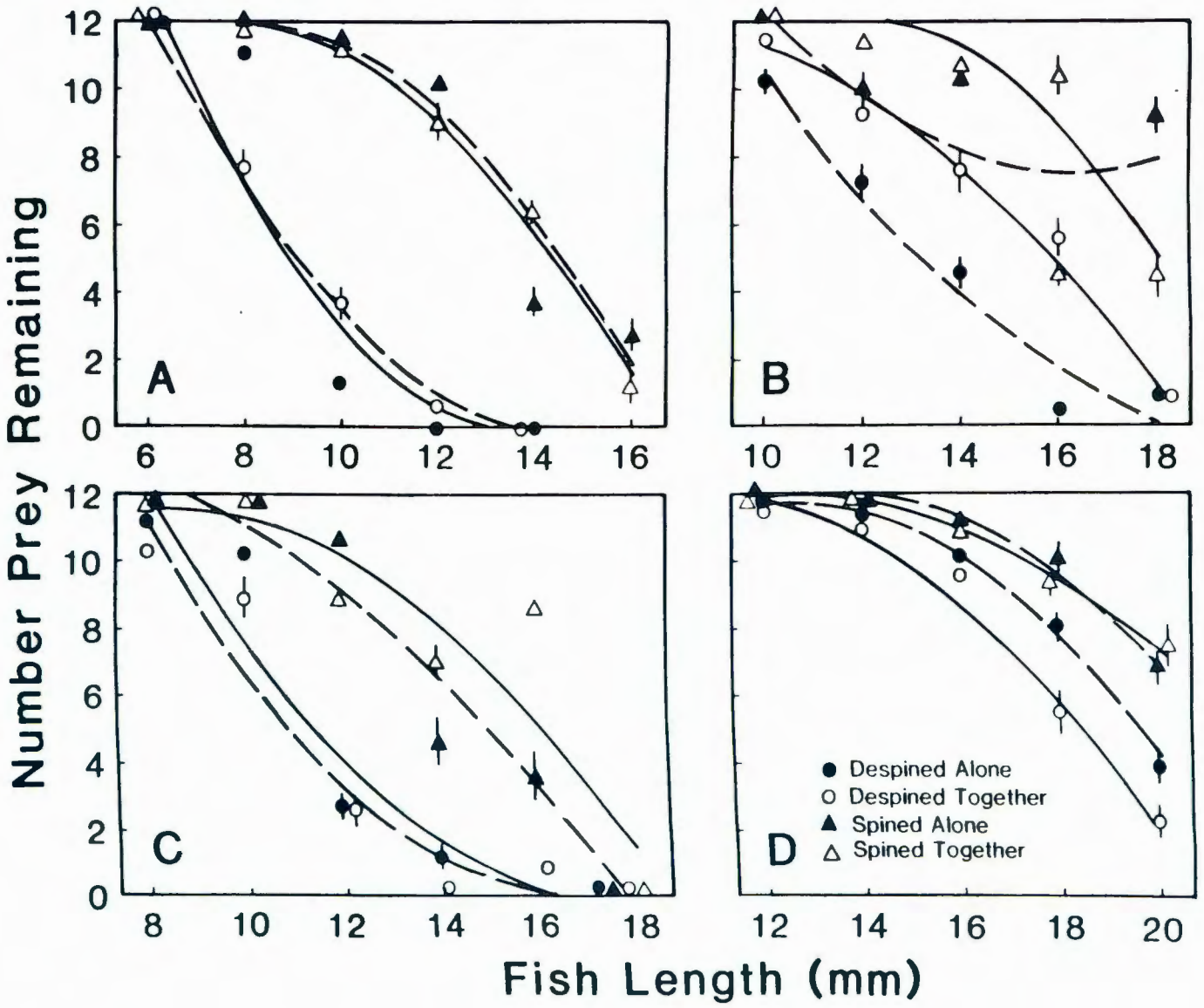

Number Prey Remaining
Fish Length (mm)
A
B
C
D
Despined Alone
Despined Together
Spined Alone
Spined Together

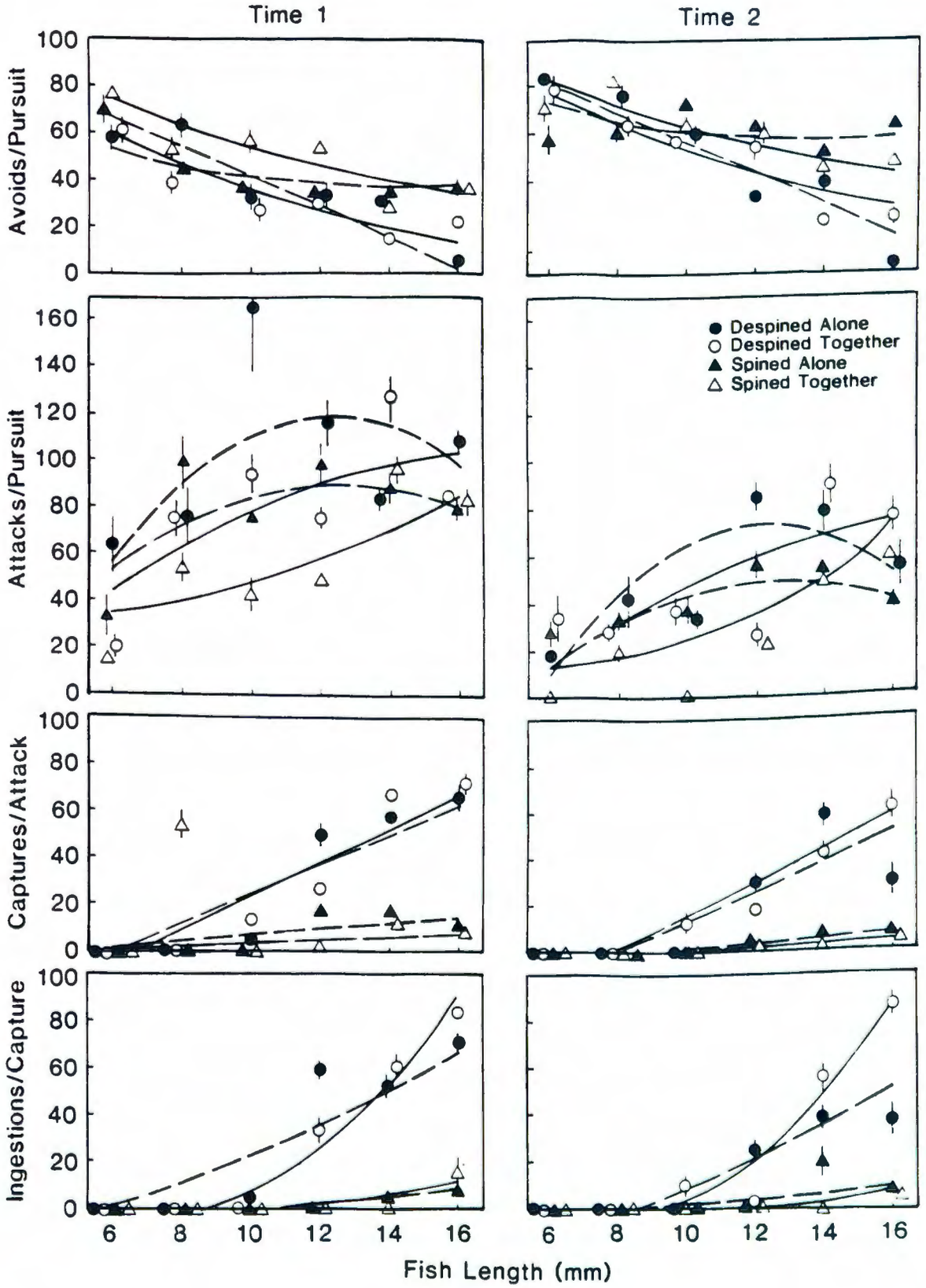
Table 2. Analysis of variance of spined (S), despined (D), and regenerating spined (R) R. harrisii zoeae (Prey) fed alone and together (Treatment) to M. menidia (Length of fish). Numerals 1-4 represent zoeal instars. Significance level: *=.05, **=.01, ***=.001.

| SOURCE | df | SS | SOURCE | df | SS |
|---|---|---|---|---|---|
| S1-D1 | 6 | 5757.73 | S1-D2 | 7 | 1739.88 |
| Prey | 1 | 1810.47*** | Prey | 1 | 429.03*** |
| Treatment | 1 | 1.67 | Treatment | 1 | 1.63 |
| Length | 1 | 3763.04*** | Length | 1 | 864.61*** |
| Length2 | 1 | 4.95 | Length2 | 1 | 14.50 |
| P X L | 1 | 48.89** | P X L | 1 | 43.51* |
| P X L2 | 3 | 623.16*** | P X L2 | 1 | 44.20* |
| Error | 233 | 1020.52 | P X T | 1 | 70.53** |
| | | | Error | 112 | 1020.03 |
| S2-D2 | 7 | 4881.21 | S1-D3 | 5 | 796.10 |
| Prey | 1 | 969.41*** | Prey | 1 | 40.83 |
| Treatment | 1 | 1.84 | Treatment | 1 | 24.30 |
| Length | 1 | 3760.72*** | Length | 1 | 588.61*** |
| Length2 | 1 | 8.80 | Length2 | 1 | 82.84** |
| P X L2 | 1 | 323.48*** | P X L | 1 | 59.51* |
| T X L | 1 | 28.60* | Error | 114 | 1343.60 |
| P X T | 1 | 31.54* | | | |
| Error | 232 | 1464.08 | S1-D4 | 5 | 706.15 |

Table 2. (continued)

| | | |
|---|---|---|
| S3-D3 | 7 | 2564.99 |
| Prey | 1 | 662.48*** |
| Treatment | 1 | 243.63*** |
| Length | 1 | 1482.25*** |
| Length2 | 1 | 2.06 |
| P X L | 1 | 139.24*** |
| T X L2 | 1 | 140.00*** |
| P X T | 1 | 35.28* |
| Error | 192 | 1431.89* |
| | | |
| S4-D4 | 5 | 1512.72 |
| Prey | 1 | 190.13*** |
| Treatment | 1 | 21.13* |
| Length | 1 | 1095.61*** |
| Length2 | 1 | 109.83*** |
| P X L | 1 | 96.04*** |
| Error | 194 | 926.63 |
| Prey | 1 | 294.53*** |
| Treatment | 1 | 12.03 |
| Length | 1 | 281.25*** |
| Length2 | 1 | 4.27 |
| P X L | 1 | 72.20* |
| Error | 114 | 1283.72 |
| | | |
| S3-R3 | 3 | 330.27 |
| Prey | 1 | 4.27* |
| Length | 1 | 193.60*** |
| Length2 | 1 | 0.30 |
| Error | 53 | 506.80 |
| | | |
| S4-R4 | 5 | 301.50 |
| Prey | 1 | 20.83* |
| Treatment | 1 | 145.20*** |
| Length | 1 | 94.61*** |
| Length2 | 1 | 3.04 |
| T X L | 1 | 37.81** |
| Error | 114 | 500.20 |

Figure 3. Percent occurrence of behaviors resulting from feeding trials with *M. menidia* 6-16 mm long and despined and spined first instar *R. harrisii* zoeae during two consecutive five minute periods. Zoeae were fed to fish separately or together.


Time 1
Time 2
Avoids/Pursuit
Attacks/Pursuit
Captures/Attack
Ingestions/Capture
Despined Alone
Despined Together
Spined Alone
Spined Together
Fish Length (mm)

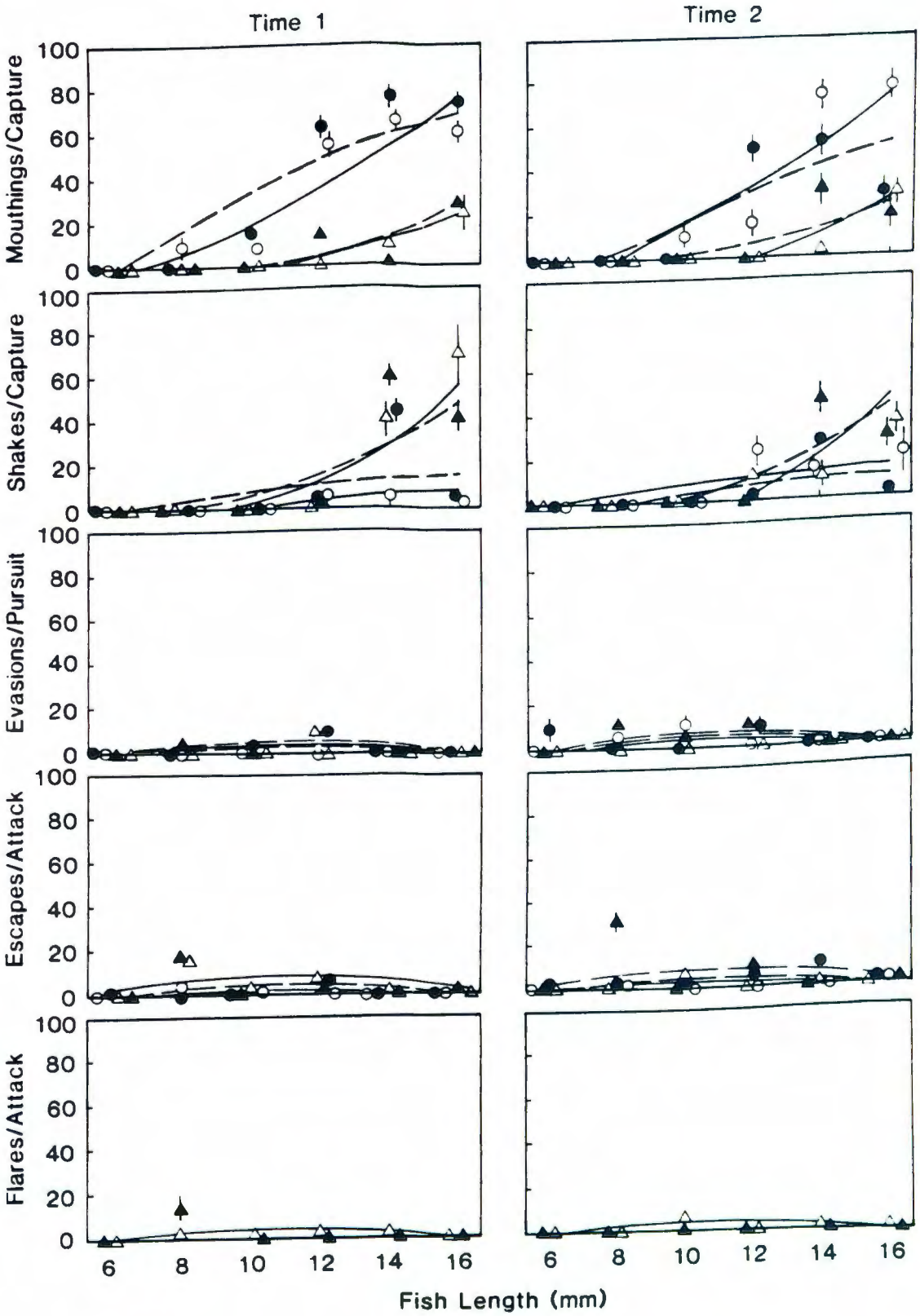

Time 1
Time 2
Mouthings/Capture
Shakes/Capture
Evasions/Pursuit
Escapes/Attack
Flares/Attack
0
20
40
60
80
100
6
8
10
12
14
16
Fish Length (mm)

Table 3. Analysis of variance of behavioral interactions between spined and despined first instar R. harrisii zoeae (Prey) fed alone and together (Treatment) to M. menidia (Length) during two consecutive five minute periods. Significance: *=.05, **=.01, ***=.001.

| SOURCE | df | SS | SOURCE | df | SS |
|---|---|---|---|---|---|
| Avoids/Pur | 7 | 1140.30 | Mouthings/Cap | 9 | 369.75 |
| Prey | 1 | 227.45*** | Prey | 1 | 549.86*** |
| Treatment | 1 | 0.71 | Treatment | 1 | 31.58* |
| Time | 1 | 134.50*** | Time | 1 | 79.01*** |
| Length | 1 | 588.02*** | Length | 1 | 1806.75*** |
| Length2 | 1 | 0.02 | Length2 | 1 | 25.88 |
| P X L | 1 | 167.32*** | P X L | 1 | 445.77*** |
| Time X L2 | 1 | 33.16* | P X L2 | 1 | 35.47* |
| Error | 472 | 3175.96 | Trt X L2 | 1 | 46.93* |
| | | | P X Time | 1 | 39.90* |
| Attacks/Pur | 7 | 2310.63 | Error | 470 | 3327.76 |
| Prey | 1 | 87.01** | | | |
| Treatment | 1 | 132.11*** | Shakes/Cap | 8 | 1122.72 |
| Time | 1 | 588.20*** | Prey | 1 | 5.56 |
| Length | 1 | 1118.06*** | Treatment | 1 | 14.26 |
| Length2 | 1 | 184.57*** | Time | 1 | 24.21 |
| Trt X L2 | 1 | 68.44* | Length | 1 | 755.00*** |
| Time X L2 | 1 | 85.28** | Length2 | 1 | 42.93* |

Table 3. (continued)

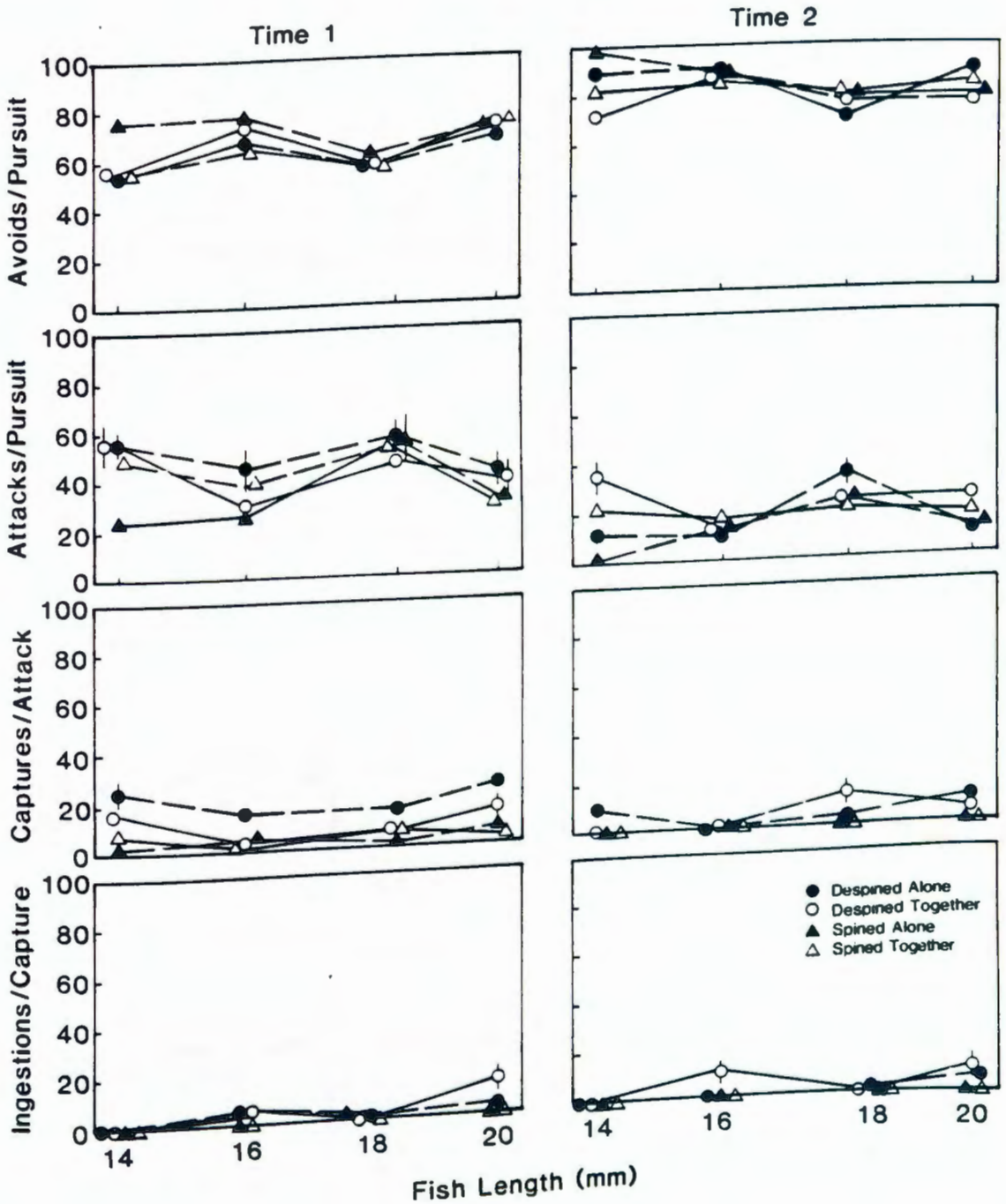
| | | |
|---|---|---|
| Error | 472 | 5425.64 |
| | | |
| Captures/Att | 9 | 3075.56 |
| Prey | 1 | 761.93*** |
| Treatment | 1 | 13.32 |
| Time | 1 | 102.28*** |
| Length | 1 | 1633.15*** |
| Length2 | 1 | 1.93 |
| P X L | 1 | 476.29*** |
| Trt X L2 | 1 | 18.39* |
| Time X L | 1 | 60.76*** |
| P X Trt | 1 | 20.49* |
| Error | 470 | 1744.79 |
| | | |
| Ingestions/Cap | 9 | 3275.55 |
| Prey | 1 | 895.91*** |
| Treatment | 1 | 26.53* |
| Time | 1 | 37.38** |
| Length | 1 | 1370.19*** |
| Length2 | 1 | 81.89*** |
| P X L | 1 | 784.75*** |
| Trt X L2 | 1 | 43.04*** |
| Time X L | 1 | 22.57* |
| P X Time | 1 | 39.77** |
| Error | 470 | 2159.94 |

| | | |
|---|---|---|
| P X L | 1 | 114.64*** |
| P X L2 | 1 | 84.17*** |
| Time X L | 1 | 37.08* |
| Error | 471 | 3076.69 |
| | | |
| Evasions/Pur | 5 | 24.08 |
| Prey | 1 | 0.05 |
| Treatment | 1 | 5.03 |
| Time | 1 | 2.55 |
| Length | 1 | 5.01 |
| Length2 | 1 | 11.43* |
| Error | 474 | 1010.64 |
| | | |
| Escapes/Att | 5 | 80.49 |
| Prey | 1 | 18.45** |
| Treatment | 1 | 26.65** |
| Time | 1 | 0.19 |
| Length | 1 | 6.79 |
| Length2 | 1 | 28.43*** |
| Error | 474 | 1213.10 |
| | | |
| Flares/Att | 7 | 30.93 |
| Prey | 1 | 10.77*** |
| Treatment | 1 | 6.88*** |
| Time | 1 | 1.30 |
| Length | 1 | 0.68 |

Table 3. (continued)

| | | |
|---|---|---|
| Length2 | 1 | 2.72* |
| P X L2 | 1 | 6.88*** |
| Error | 472 | 247.84 |

Figure 4. Percent occurrence of behaviors resulting from feeding trials with *M. menidia* 14-20 mm long and despined and spined fourth instar *R. harrisii* zoeae during two consecutive five minute periods. Zoeae were fed to fish separately or together.


Time 1
Time 2
Avoids/Pursuit
Attacks/Pursuit
Captures/Attack
Ingestions/Capture
100
80
60
40
20
0
14
16
18
20
Fish Length (mm)
Despined Alone
Despined Together
Spined Alone
Spined Together

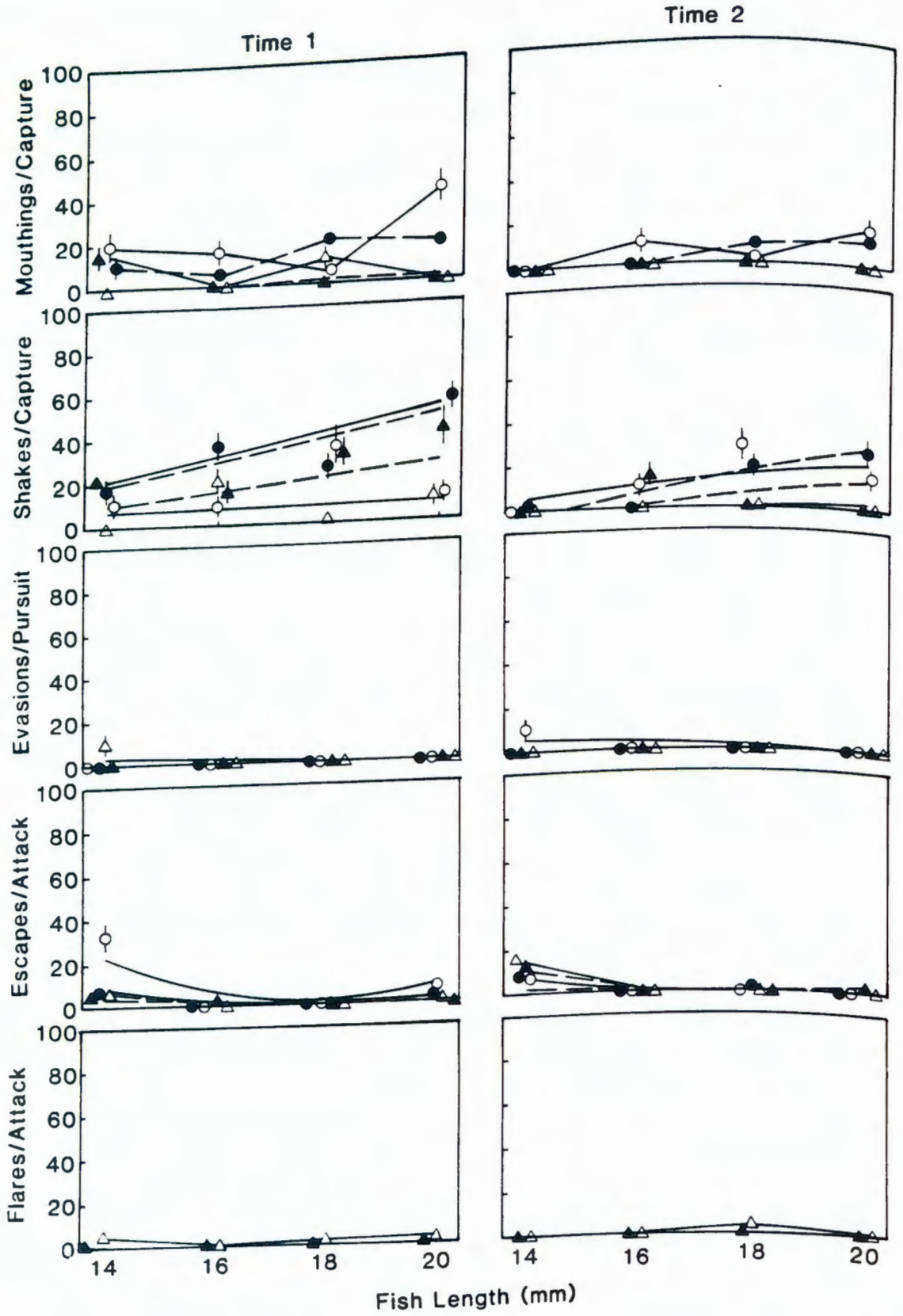

Time 1
Time 2
Mouthings/Capture
Shakes/Capture
Evasions/Pursuit
Escapes/Attack
Flares/Attack
0
20
40
60
80
100
14
16
18
20
Fish Length (mm)

Table 4. Analysis of variance of behavioral interactions between spined and despined fourth instar R. harrisii zoeae (Prey) fed alone and together (Treatment) to M. menidia (Length) during two consecutive five minute periods (Time). Significance: *=.05, **=.01, ***=.001.

| SOURCE | df | SS | SOURCE | df | SS |
|---|---|---|---|---|---|
| Avoids/Pur | 6 | 140.50 | Shakes/Cap | 6 | 571.42 |
| Prey | 1 | 8.29* | Prey | 1 | 138.49*** |
| Treatment | 1 | 11.87* | Treatment | 1 | 103.14*** |
| Time | 1 | 117.02*** | Time | 1 | 135.07*** |
| Length | 1 | 0.06 | Length | 1 | 77.46** |
| Length2 | 1 | 0.96 | Length2 | 1 | 1.83 |
| Trt X L | 1 | 8.03* | Trt X Time | 1 | 58.09* |
| Error | 312 | 571.19 | Error | 312 | 2803.74 |
| | | | | | |
| Attacks/Pur | 7 | 576.59 | Evasions/Pur | 6 | 8.24 |
| Prey | 1 | 14.97 | Prey | 1 | 0.00 |
| Treatment | 1 | 4.85 | Treatment | 1 | 2.61* |
| Time | 1 | 477.64*** | Time | 1 | 1.26 |
| Length | 1 | 10.54 | Length | 1 | 3.37* |
| Length2 | 1 | 15.11 | Length2 | 1 | 1.26 |
| Trt X L | 1 | 40.06** | Error | 312 | 189.92 |
| Trt X L2 | 1 | 20.27* | | | |
| Error | 311 | 1598.27 | Escapes/Att | 9 | 223.66 |

Table 4. (continued)

| | | |
|---|---|---|
| Captures/Attack | 5 | 320.00 |
| Prey | 1 | 136.35*** |
| Treatment | 1 | 16.44* |
| Time | 1 | 140.40*** |
| Length | 1 | 0.20 |
| Length2 | 1 | 14.37 |
| Error | 313 | 1252.41 |
| | | |
| Ingestions/Cap | 5 | 36.08 |
| Prey | 1 | 20.53*** |
| Treatment | 1 | 0.00 |
| Time | 1 | 1.04 |
| Length | 1 | 3.56 |
| Length2 | 1 | 0.66 |
| Error | 313 | 517.94 |
| | | |
| Mouthings/Cap | 5 | 220.38 |
| Prey | 1 | 5.53*** |
| Treatment | 1 | 5.48*** |
| Time | 1 | 1.34 |
| Length | 1 | 0.13 |
| Length2 | 1 | 0.26 |
| Prey | 1 | 0.45 |
| Treatment | 1 | 0.07 |
| Time | 1 | 13.55* |
| Length | 1 | 151.63*** |
| Length2 | 1 | 84.00*** |
| P X L | 1 | 19.30** |
| P X L2 | 1 | 11.18* |
| Trt X L | 1 | 21.07** |
| Trt X L2 | 1 | 15.91** |
| Error | 309 | 643.60 |
| | | |
| Flares/Att | 5 | 2.53 |
| Prey | 1 | 5.53*** |
| Treatment | 1 | 5.48*** |
| Time | 1 | 1.34 |
| Length | 1 | 0.13 |
| Length2 | 1 | 0.26 |
| Error | 313 | 12.65 |

Figure 5. Number of first instar despined and spined remaining after being fed together to F. heteroclitus 6-10 mm long for 24 h.

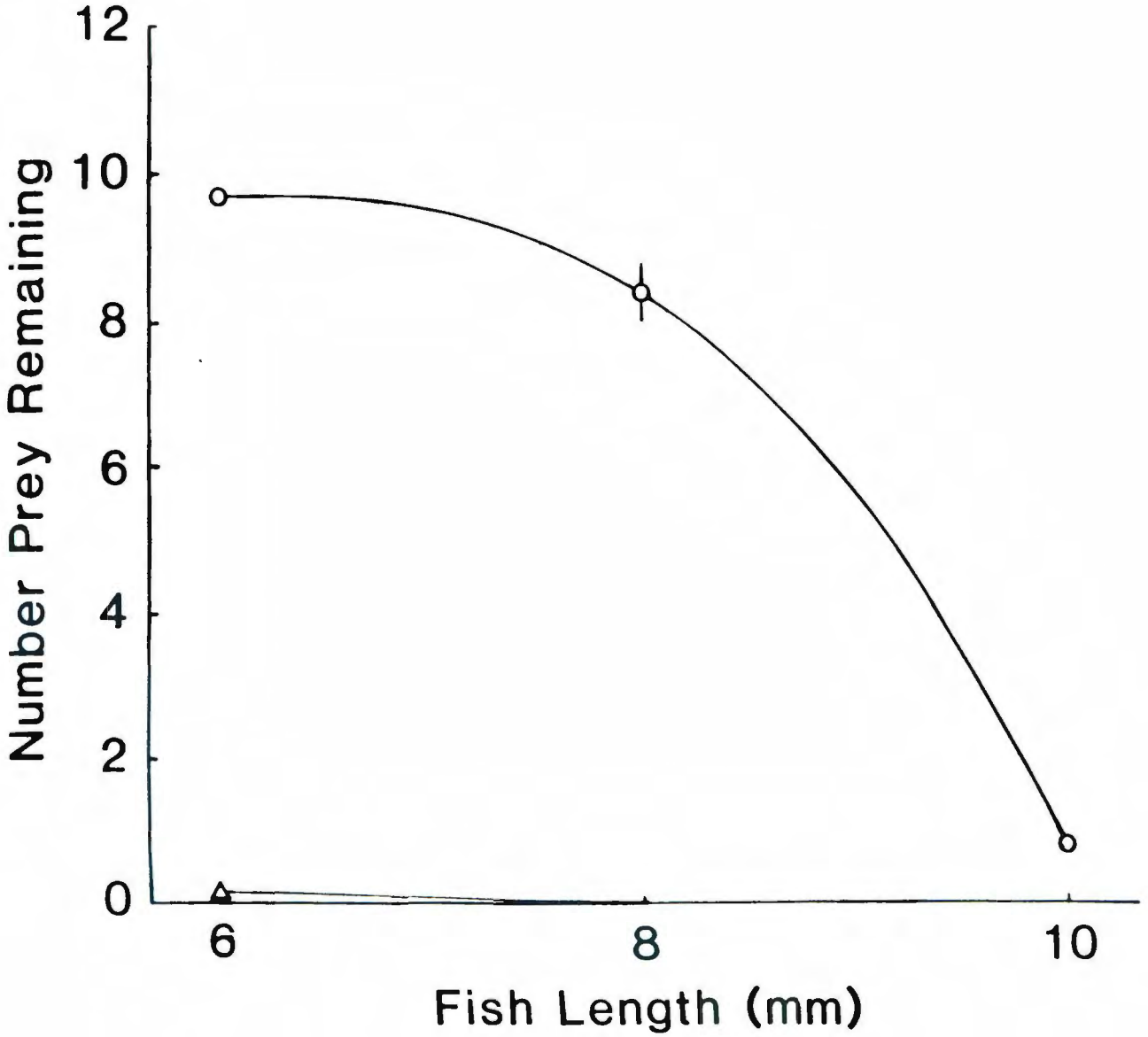

12
10
8
6
4
2
0
Number Prey Remaining
6
8
10
Fish Length (mm)

Table 5. Analysis of variance of behavioral interactions between spined and despined first instar R. harrisii zoeae (Prey) fed together to F. heteroclitus (Length) during two consecutive five minute periods (Time). Significance: *=.05, **=.01, ***=.001.

| SOURCE | df | SS | SOURCE | df | SS |
|---|---|---|---|---|---|
| Avoids/Pur | 4 | 190.04 | Attacks/Pur | 5 | 1086.45 |
| Prey | 1 | 0.56 | Prey | 1 | 193.94** |
| Time | 1 | 161.52*** | Time | 1 | 739.98*** |
| Length | 1 | 5.67 | Length | 1 | 1.11 |
| Length2 | 1 | 21.95 | Length2 | 1 | 0.56 |
| Error | 113 | 848.34 | P X T | 1 | 139.93* |
| | | | Error | 112 | 2882.88 |
| Captures/Att | 4 | 361.64 | Ingestions/Cap | 6 | 554.04 |
| Prey | 1 | 117.01** | Prey | 1 | 263.96*** |
| Time | 1 | 36.86 | Time | 1 | 36.61* |
| Length | 1 | 194.30*** | Length | 1 | 73.39** |
| Length2 | 1 | 7.29 | Length2 | 1 | 78.74** |
| Error | 113 | 1596.51 | P X L | 1 | 31.12* |
| | | | P X L2 | 1 | 70.64** |
| | | | Error | 111 | 801.09 |
| Mouthings/Cap | 4 | 754.01 | Shakes/Cap | 5 | 275.38 |
| Prey | 1 | 562.14*** | Prey | 1 | 207.24*** |
| Time | 1 | 150.94** | Time | 1 | 47.94 |

Table 5. (continued)

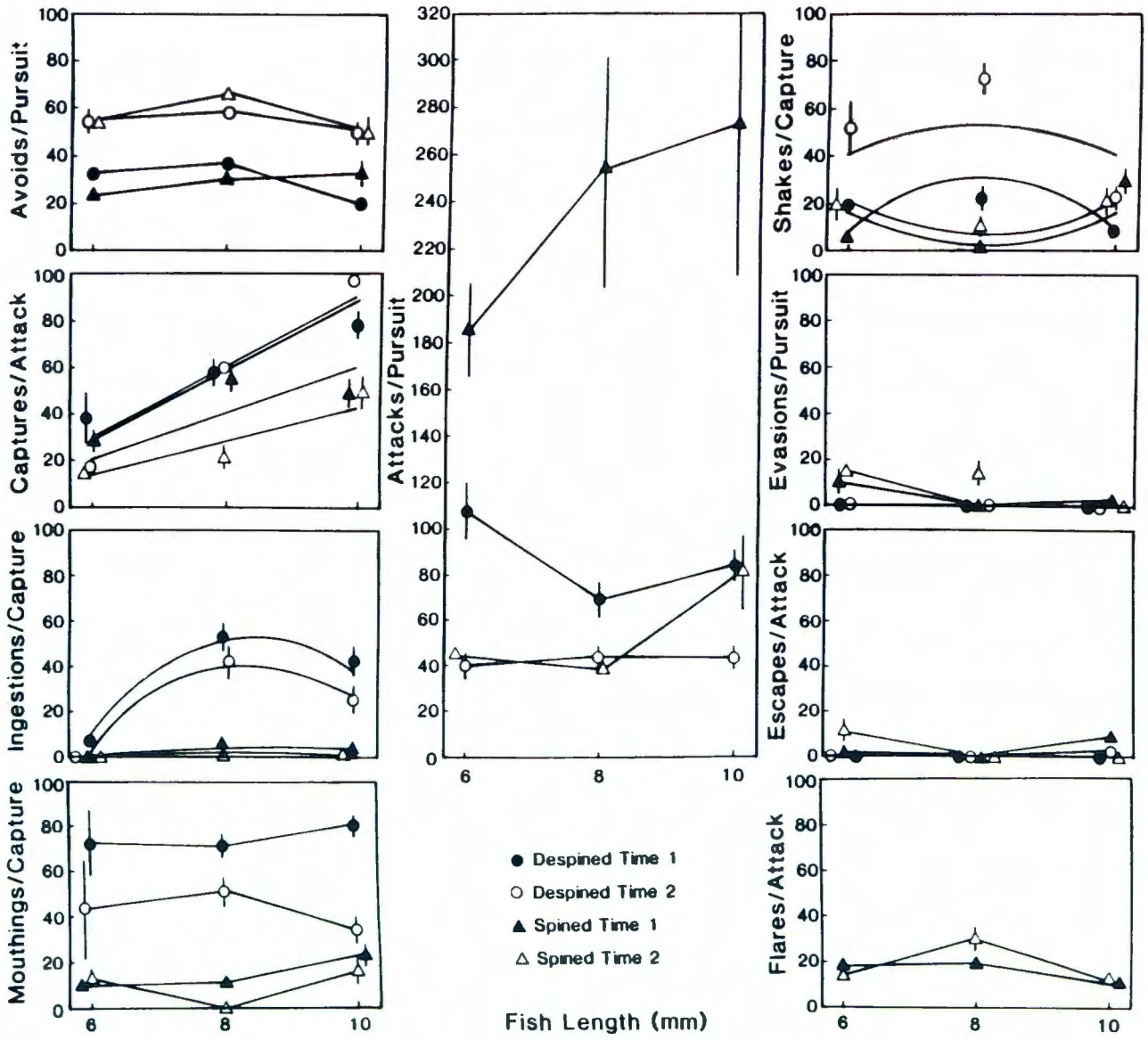
| | | | | | |
|---|---|---|---|---|---|
| Length | 1 | 33.14 | Length | 1 | 2.46 |
| Length2 | 1 | 1.19 | Length2 | 1 | 7.03 |
| Error | 113 | 1761.00 | P X L2 | 1 | 96.18* |
| | | | Error | 112 | 1574.98 |
| | | | | | |
| Evasions/Att | 4 | 19.28 | Escapes/Att | 4 | 9.45 |
| Prey | 1 | 8.10 | Prey | 1 | 4.30 |
| Time | 1 | 0.03 | Time | 1 | 0.36 |
| Length | 1 | 6.30 | Length | 1 | 0.38 |
| Length2 | 1 | 4.55 | Length2 | 1 | 4.28 |
| Error | 113 | 24.97 | Error | 113 | 207.40 |
| | | | | | |
| Flares/Att | 4 | 346.42 | | | |
| Prey | 1 | 329.21*** | | | |
| Time | 1 | 2.31 | | | |
| Length | 1 | 2.93 | | | |
| Length2 | 1 | 11.78 | | | |
| Error | 113 | 360.65 | | | |

escapes and flares by zoeae generally was greatest when prey were fed to fishes of intermediate size classes. The frequency of most behaviors for fish preying on fourth instar zoeae did not change over the range of fish lengths tested. However, the number of avoidances decreased when larvae were preyed upon by large fishes, and the number of escapes was again greatest at intermediate fish lengths.

The spines of R. harrisii zoeae also prevented killifish from preying on first instar zoeae during 24 h feeding trials (Figure 5). Killifish attacked, captured, ingested, and mouthed despined more than spined zoeae, but there was no significant difference in the frequency of avoidance of the two prey types (Figure 6, Table 5). Killifish shook spined zoeae more frequently than despined zoeae, which further indicated that spined prey posed greater difficulties. The frequency of evasion and escape by despined and spined zoeae were not signficantly different.

Killifish generally experienced less difficulty preying on spined zoeae than did silversides (Figure 6, Table 5). Killifish 6-10 mm long attacked ($df=1,118$; $F=27.98$; $p<.001$), captured ($df=1, 118$; $F=79.47$, $p<0.001$), ingested ($df=1,118$; $F=5.6$; $p=0.02$), mouthed ($df=1,118$; $F=16.28$; $p<0.001$), and shook ($df=1,118$; $F=16.48$; $p<0.001$) more first instar zoeae than silversides, but killifish also avoided them more than did silversides ($df=1,118$, $F=12.53$, $p<0.001$). There were no significant differences in the frequency of evasion ($df=1, 118$; $F=2.02$; $p=0.16$) or escape ($df=1,118$; $F=0.54$; $p=0.46$)

Figure 6. Percent occurrence of behaviors resulting from feeding trials with F. heteroclitus 6-10 mm long and despined and spined first instar R. harrisii during two consecutive five minute periods.


Avoids/Pursuit
Captures/Attack
Ingestions/Capture
Mouthings/Capture
Attacks/Pursuit
Shakes/Capture
Evasions/Pursuit
Escapes/Attack
Flares/Attack
Despined Time 1
Despined Time 2
Spined Time 1
Spined Time 2
Fish Length (mm)

by zoeae when fed to the two fishes, but zoeae fed to killifish flared their spines more often than when fed to silversides ($df=1,118$; $F=49.7$; $p<0.001$).

Noxious Spines Increase the Size of Zoeae

Noxious spines are more effective than a larger body at preventing predation on R. harrisii zoeae, within limits. The smaller body size and spines of first instar zoeae were significantly more effective at preventing fish predation than was large body size of despined second and third instar zoeae (Figure 7, Table 2). However, the spines of first instar zoeae were significantly less effective at preventing fish predation than was the large body size of fourth instar zoeae.

Spines may even kill small fishes attempting to prey on zoeae. All twelve 16 mm silversides fed only R. harrisii zoeae died within eight days, whereas all fish fed despined R. harrisii zoeae or Artemia survived. Only one starved fish died (on the last day) of the experiment. However, spines did not result in the death of any small killifish or 40 mm silversides.

Long Spines Increase Survival of Attacked Zoeae

The armor of crab zoeae enable them to withstand attacks by juvenile fish, and small zoeae bearing long spines are more likely to survive attacks than are large zoeae with short spines. Survival to postlarva of Rhithropanopeus harrisii that had been attacked by 16 mm silversides was comparable to survival of zoeae that had not been

Figure 7. Number of spined first instar zoeae remaining after 24 h when fed to *M. menidia* separately or together with A) second, B) third, and C) fourth instar despined *R. harrisii* zoeae.

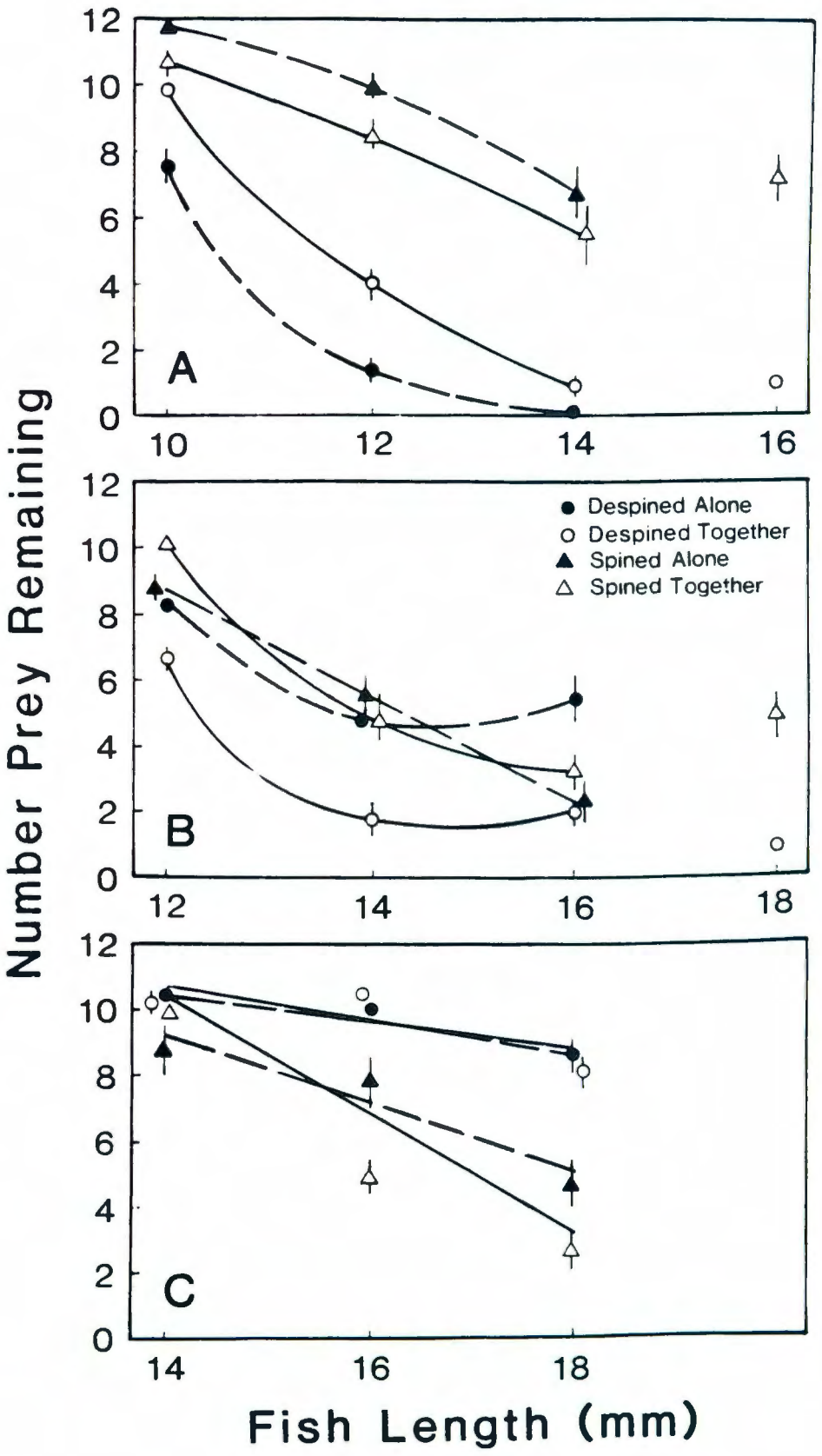
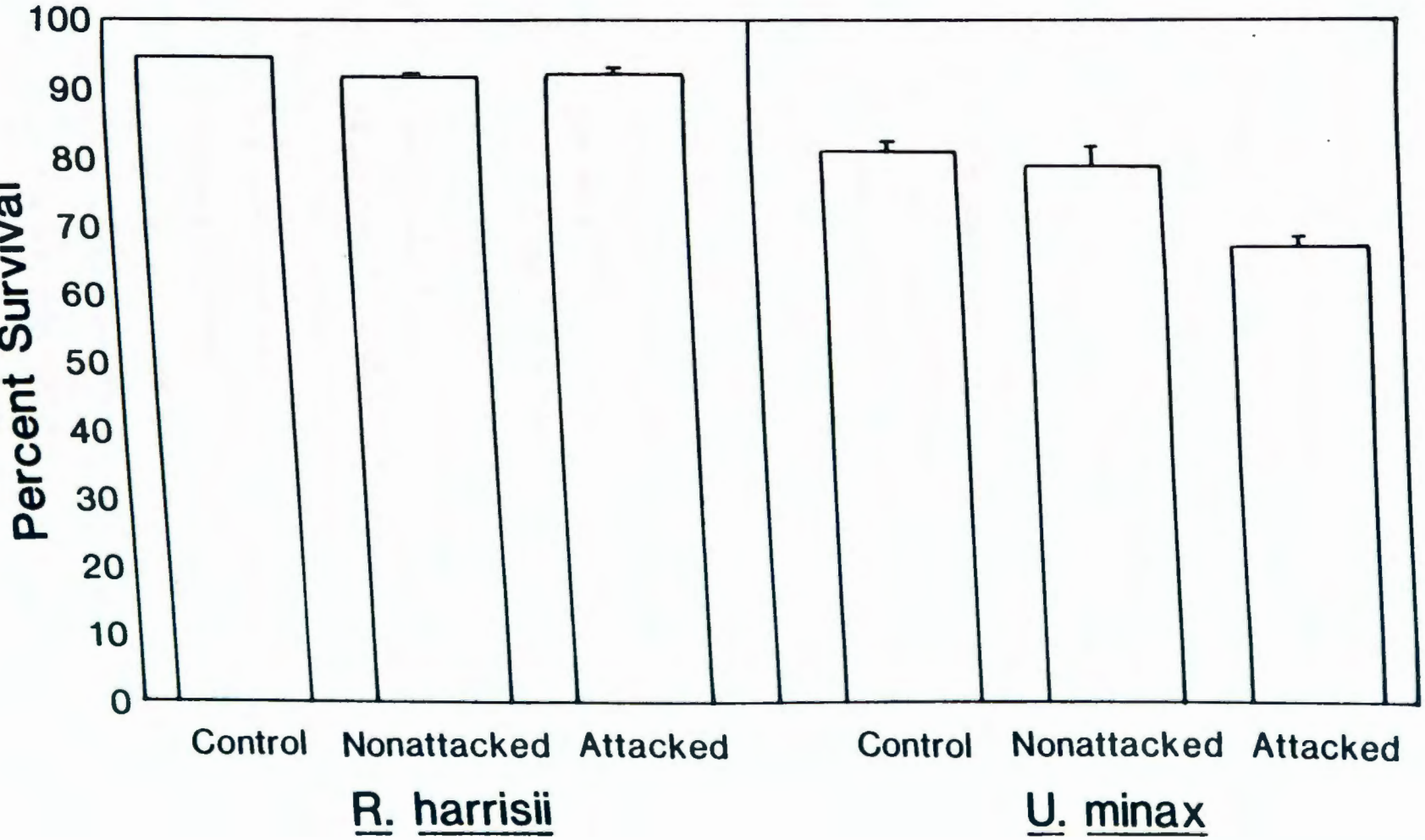

Number Prey Remaining
Fish Length (mm)
A
B
C
Despined Alone
Despined Together
Spined Alone
Spined Together
0
2
4
6
8
10
12
14
16
18

Figure 8. Percent survival to metamorphosis of R. harrisii and S. reticulatum zoeae which were attacked by M. menidia, exposed to fish but not attacked, or not exposed to fish.


Percent Survival
100
90
80
70
60
50
40
30
20
10
0
Control
Nonattacked
Attacked
Control
Nonattacked
Attacked
R. harrisii
U. minax

attacked by fish (df=2,6; F=0.12; p=0.89) (Figure 8). Sesarma reticulatum zoeae, which have shorter spines and a larger body size than R. harrisii, did not survive as well when attacked by silversides as when not attacked by fish (df=2,6; F=12.01; p=0.008). The larval development time of attacked zoeae was not extended for either species (Rhithropanopeus: df=2,6; F=2.55; p=0.16; Sesarma: df=2,6; F=1.07; p=0.40).

Examinations of zoeae that died during the course of the experiment revealed that more spines of both species of zoeae were broken during fish attacks than when not attacked (Table 6). The long spines of R. harrisii zoeae were more likely to break than the short spines of S. reticulatum. Dorsal spines of both species are more likely to break than antennal or rostral spines. Although the long spines of R. harrisii were more likely to break than those of S. reticulatum, they protected the zoeae better. None of the 360 R. harrisii zoeae attacked by fish was mangled, whereas 21 of the 360 S. reticulatum attacked by fish had mishapen bodies.

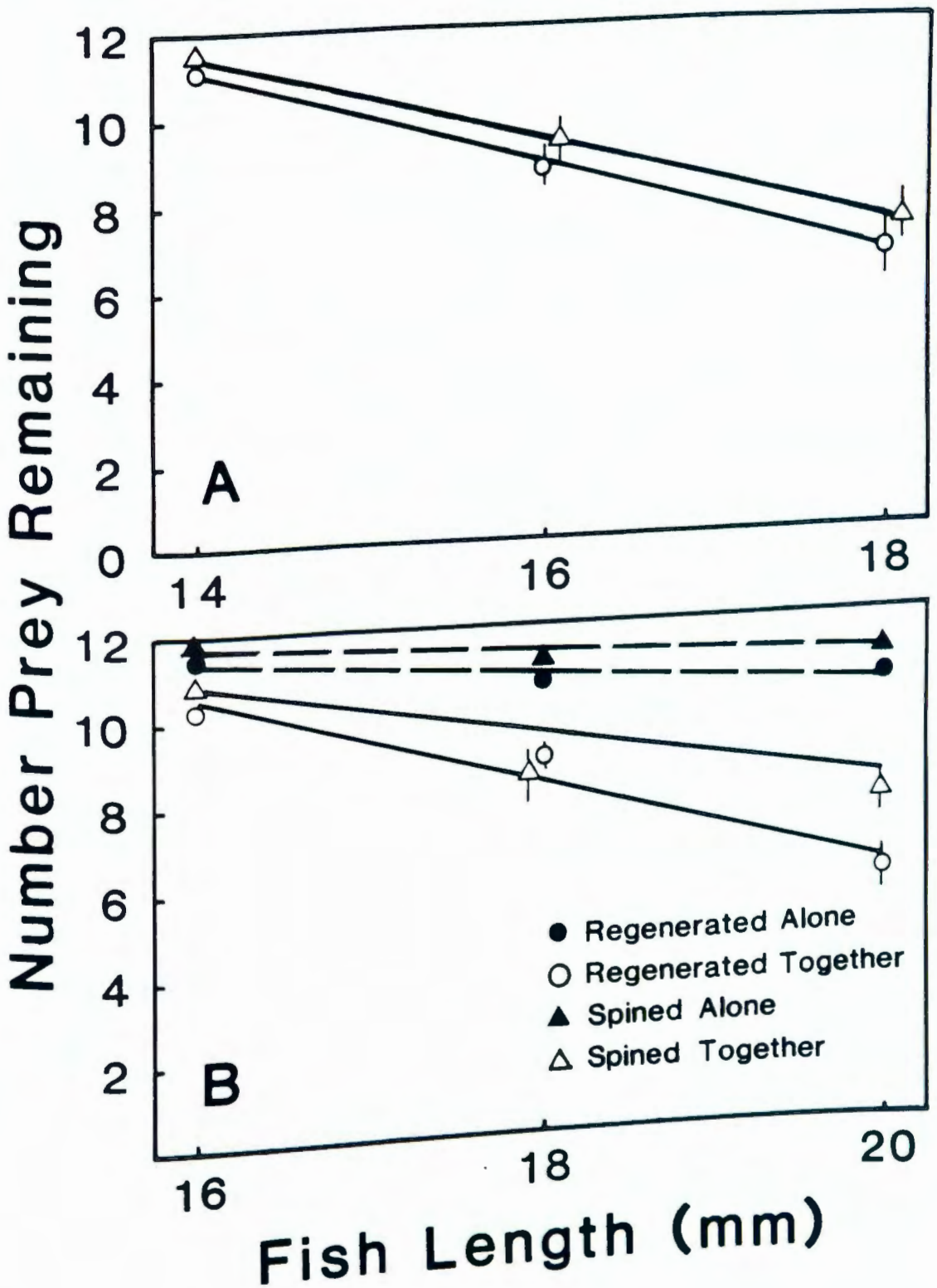
Regenerating Spines Prevent Predation

Spines in the process of regenerating are as effective at preventing predation as are unbroken spines, if the two types of prey were offered to fish simultaneously. The regenerating spines of third and fourth instar R. harrisii, which had their spines amputated during the second instar, were as effective as unbroken spines at preventing predation by small silversides when zoeae were fed simultaneously to

Table 6. Occurrence of damage to 360 *R. harrisii* and 360 *S. reticulatum* zoeae not offered to *M. menidia* (C), of zoeae offered but not attacked (N), and zoeae attacked by fish (A).

| *R. harrisii* | C | N | A |
|---|---|---|---|
| Damaged Spines | 8 | 7 | 39 |
| Dorsal | 8 | 7 | 25 |
| Rostral | 0 | 0 | 4 |
| Antennal | 0 | 0 | 10 |
| Mangled Bodies | 0 | 0 | 0 |
| *S. reticulatum* | | | |
| Damaged Spines | 0 | 0 | 11 |
| Dorsal | 0 | 0 | 7 |
| Rostral | 0 | 0 | 1 |
| Antennal | 0 | 0 | 3 |
| Mangled Bodies | 0 | 0 | 21 |

Figure 9. Number of A) third and B) fourth instar R. harrisii zoeae with partially regenerated or normal spines. Zoeae were fed separately or together to fish.


Number Prey Remaining
12
10
8
6
4
2
0
A
14
16
18
12
10
8
6
4
2
B
16
18
20
Fish Length (mm)
Regenerated Alone
Regenerated Together
Spined Alone
Spined Together

fish. (Figure 9, Table 2). However, larger fish preferred fourth instar zoeae with regenerating spines to those with unbroken spines when they were fed separately to fish.

Discrimination of Spined Prey by Small Fishes and Learning

The percentage of attacks per pursuit by silversides and killifish was much greater for first instar despined than spined larvae, and the percentage of avoidances per pursuit by silversides was least for first instar despined zoeae (Table 3, 5). Because fishes preferred despined to spined zoeae they must be able to discriminate between them. However, results of feeding trials designed to distinguish if larval fishes can discriminate between spined and spineless prey were inconclusive. Significant interactions between the type of prey fed to fish and whether or not they were fed alone or together occurred in only three of eight feeding trials and only once during the observation periods. Only one of the three feeding experiments showed that more despined zoeae were eaten when fed alone than together with spined zoeae, without the number of spined zoeae consumed by fish being significantly different (Table 2). The difference in the number of spined zoeae eaten when fed separately versus together to fish during the observation period was greater than the difference in the number of despined zoeae consumed when fed alone versus together and does not support the hypothesis that fish can detect zoeal spines (Table 3, 4).

The frequency of fish behaviors usually changed with

exposure time, but zoeal behavior did not (Tables 3, 4, 5). Fish generally avoided despined and spined zoeae more frequently during the first than the second five minute observation period, but attacked, captured, mouthed, and swallowed zoeae less often as exposure time increased (Figures 3, 4, 5). Fish were very hungry at the conclusion of the observation period, but zoeae still remained uneaten. Therefore fish learned to avoid both types of zoeae. However, fish preferences for despined over spined zoeae did not increase from the first to the second observation period.

Spines and Invertebrate Predation

Spines were not effective at deterring predation by most invertebrates. Of the ten invertebrates tested, only the hydrozoan medusa, Eutima mira, preyed upon significantly fewer spined than despined zoeae (Figure 10, Table 7).

Spines as Stabilizing or Flotation Devices

The elongate spines of R. harrisii did not assist in the flotation of the zoeae unless the antennal spines were flared perpendicularly to their resting position (Figure 11). Despined zoeae sank as quickly as spined zoeae, but faster than did those with their spines splayed (SNK, $df=2,147$; $t=6.73$; $p<0.05$). Nor did spines stabilize R. harrisii zoeae. Despined and spined zoeae with their spines flared or in the resting postition all sink upside down without oscillating sideways.

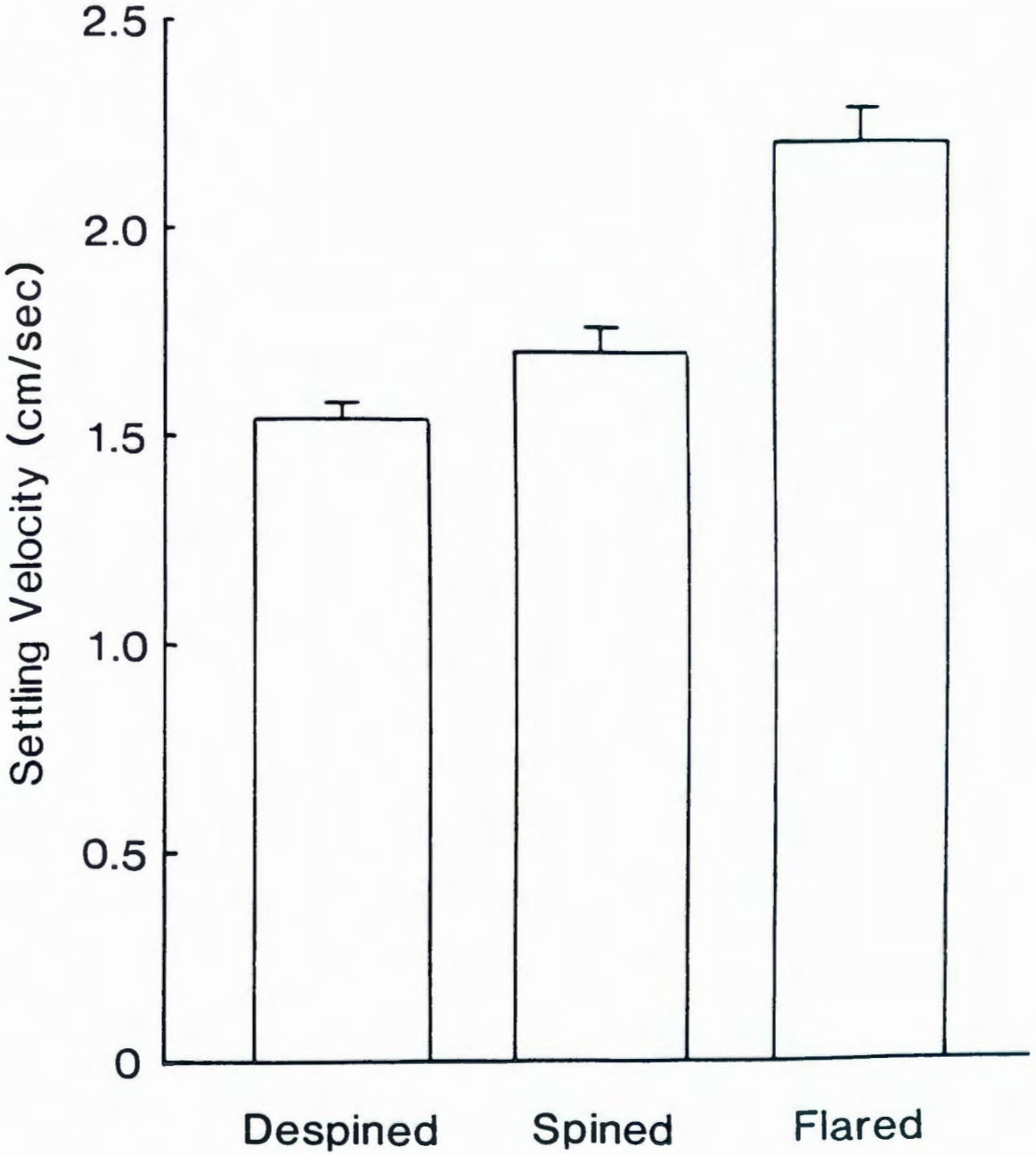
Figure 10. Number of spined and despined zoeae surviving after exposure to ten planktonic and benthic invertebrate predators.

Mean No. Surviving Larvae
0
5
10
15
20
25
30
35
S. hispida
E. mira
M. leidyi
S. plicata
A. pallida
B. amphitrite
C. penantis
P. pugio
R. harrisii
G. demissa
Spined R. harrisii
Despined R. harrisii

Table 7. Analysis of variance of invertebrate predation on spined and despined *R. harrisii* larvae.

| PREDATOR | MS | F | P |
|---|---|---|---|
| *Sagitta hispida* | 38.00 | 3.59 | .07 |
| *Eutima mira* | 45.63 | 29.13 | .0001 |
| *Mnemiopsis leidyi* | 49.00 | 0.45 | .51 |
| *Styela plicata* | 26.45 | 4.16 | .06 |
| *Aiptasia pallida* | 80.00 | 1.88 | .19 |
| *Balanus amphitrite* | 5.89 | 0.13 | .72 |
| *Caprella penantis* | 0.44 | 0.06 | .80 |
| *Geukensia demissa* | 1.13 | 0.19 | .67 |

Figure 11. Settling velocity of R. harrisii with spines removed, resting in their normal position, or flared perpendiculary to their body.


Settling Velocity (cm/sec)
2.5
2.0
1.5
1.0
0.5
0
Despined
Spined
Flared

# DISCUSSION

## Selection for Zoeal Spines

Spines of crab zoeae appear to have been selected primarily to prevent predation by small fishes rather than by invertebrate predation, and do not appear to have evolved to assist in the flotation or stabilization of the organism. Neither despined nor spined zoeae oscillated while sinking in a settling tube or during brief periods of passive sinking following attacks by fishes. Nor were spines needed to stabilize the zoeae while swimming, as suggested by Weldon (1889). Zoeae often swam erratically following the amputation of their spines as noted by Weldon, but zoeae quickly regained their normal orientation.

Spines did not appear to assist in the flotation of the zoeae, because despined and spined zoeae sank at the same rate. Cladocerans with helmets and longer spines actually sink faster than nonexuberant cladocerans (Dodson, 1984), so that spines of crustacean zooplankters do not appear to have evolved to assist in flotation. However, if zoeae flare their spines to retard sinking, then spines could also have evolved as a flotation device. But in the six years I have reared and experimented with R. harrisii zoeae, I have never seen them splay their spines while swimming unless attacked. Furthermore, trochophores and rotifers appear to flare their spines only following attack (Gilbert, 1967; Cowden et al., 1984; Pennington and Chia, 1984).

Despite the various feeding modes of the ten inverte-

brates fed zoeae, spines were effective at deterring predation by only one predator. However, spines were effective against both large-mouthed, bottom-feeding and small-mouthed planktivorous species of fishes. The fitness of zoeae possessing spines clearly is increased because spines limit the size at which fishes can begin preying on zoeae and protect zoeae which are attacked by fishes. Zoeae were sometimes attacked over thirty times in quick succession but still swam away. Long-spined zoeae that were attacked had the same survival and duration to metamorphosis as did zoeae that were not attacked, indicating that attacked zoeae are more likely to survive and reproduce than were zoeae bearing short spines or no spines at all. Therefore, predation by small fishes should create strong selective pressure for increasing spine length.

A further indication of the importance of spines is revealed by the fact that R. harrisii zoeae entirely regenerate a lost dorsal spine within two molts (Freeman, 1983), even though its larval development only includes four molts over a 12 day period at 25 oC (Costlow et al., 1966). Dorsal spines were broken most frequently during attacks. When all spines were removed, spines regenerated in one or two molts did not regain their initial length, but were as effective as undamaged spines at preventing fish predation even after only one molt. The cost of producing zoeal spines may be slight because they are composed only of epidermis, hemolymph and cuticle (Freeman, 1983). Jacobs

(1967 cited in Riessen, 1984) has calculated that the cost of growing helmets and spines to cladocerans is slight. However, the assymetrical growth of the posterior spines of cyclomorphic rotifers may indicate that there is a cost to spine production, provided one spine is as effective as two in deterring predation (Gilbert and Stemberger, 1984). The decreased survival, fecundity and growth rates of cyclomorphlic cladocerans (Kerfoot, 1977b; O'Brien et al., 1980; Riessen, 1984) may not be due to the energy allocated to the production of spines and helmets as much as to the concurrent lateral compression of the body. A slender body results in a smaller brood chamber and decreased feeding efficiency (Riessen, 1984).

Selection should be intensified even further because there can be strong selection against fish preying on long spined zoeae, as well as for zoeae to bear spines. Silversides preying exclusively on R. harrisii zoeae died when zoeae with flared spines became lodged in their pharynx. Lebour (1919) also determined that the dorsal spine of a megalopa caused the prey to become wedged in the esophagus of a small fish, resulting in its death. Presumably the large mouths of killifish and large silversides are better able to handle armored prey, because they did not die when feeding on zoeae. Killifish and large silversides occassionally feed on armored prey, such as crabs, shrimp, and snails (Kneib and Stiven, 1978).

Furthermore, behavioral observations indicated that

small fishes can distinguish between spined and despined zoeae and quickly learn to avoid spined zoeae, which would enhance the effectiveness of spines as an antipredatory adaptation as well as the rate of evolution of the trait. Spined zoeae of both instars tested were avoided more and attacked less often than were despined zoeae during the ten-minute feeding trials. Thus, fish larvae, as well as adults, actively choose to attack based on characteristics of the prey and previous success in capturing the prey. This also means that fish larvae are able to detect structural detail, despite having inferior visual acuity. Hessen (1985) found that the amount of pigmentation, rather than antennal length, mucron length, or eggs, determined whether one morph of cladoceran would be selected by fish over another, but none of these structures limited predation as did spines. Spines clearly prevented fish from preying on zoeae, as well as inhibiting some fish from attempting to swallow zoeae. Thus, fish appear to actively choose prey based on fine morphological structures. However, experiments designed as a further test of the discriminative behavior of fish were inconclusive. The number of despined zoeae eaten when fed together or separately to fish did not change in any manner consistent with the hypothesis that fish can distinguish spined from despined zoeae. Nor was fish behavior different towards despined or spined zoeae when they were fed separately or together to fish during the 10-minute observation periods. This experimental design may

be more effective at detecting discriminatory and learning ability when preferred prey are used in opposition to noxious prey, rather than when prey merely differ in the extent of their unpalatability to the predator.

Fish preference for zoeae did not change from the first to the second five minutes, indicating that preferences were established in less than five minutes. Aggregations of zooplankters might be encountered frequently in patchily distributed plankton communities, and could hasten learning by fish to avoid noxious prey or to take advantage of palatable prey (Bohl, 1982; Dill, 1983; Bronmark et al., 1984). Kerfoot et al. (1980) also found short term as well as long term learning in the avoidance of distasteful water mites.

In addition to their noxious qualities, spines operate by effectively increasing the size of zoeae. The total size of first instar R. harrisii zoeae, from the tip of the dorsal to the tip of the rostral spines is 2 mm, but without spines the body size is only 0.4 mm. Thus, spines quintuple the size of the zoeae. Following attack, zoeae flare their antennal spines perpendicularly to the plane formed by the rostral and dorsal spines, so that spines increase the size of the zoeae in all directions. Rhithropanopeus harrisii zoeae further increase their size by flexing the abdomen back over the carapace, and in so doing a pair of abdominal spines become erect. Zoeae remain motionless in this position until fish lose interest,

whereupon they collapse their spines and resume swimming. Lindstrom (1955) also found that fish lose interest in motionless prey. Trochophores also erect setae when attacked (Cowden et al., 1984; Pennington and Chia, 1984), and amphipods prevent fish predation by bending backwards with their legs and antennae sticking out (Magnahagen and Wiederholm, 1982). Adult stomatopods flex their abdomens up and back, projecting lateral spines on the sides of the body and uropods (M. Reaka, pers. comm.). Amphipods and trochophores also remain motionless while in their defensive postures (Cowden et al., 1984; Magnhagen, 1985). However, spines are better than large body size at preventing predation due to their noxious properties.

Although the ratio of spine length to body size remains constant throughout development, the effectiveness of spines at preventing predation relative to body size appears to diminish with each successive instar. Thus, spines appear to be most effective at preventing predation by small fishes on small zoeae, and their effectiveness diminishes as both the zoeae and their fish predators increase in size. The efficiency of prey capture generally increases as fish develop (Durbin, 1979; Hunter, 1980; Unger and Lewis, 1983).

Spines appear to absorb the brunt of attacks by fish and may break, but leave the body undamaged if they are long enough. Sea urchin spines also may break while effectively protecting the tests of urchins (Strathmann, 1981). The long spines and small body size of R. harrisii zoeae rather

than the short spines and large body size of S. reticulatum were more effective at preventing fatalities of attacked zoeae. Spine length may be correlated with exoskeleton thickness or rigidity (Dodson, 1984), which might also account for the greater survival of R. harrisii than S. reticulatum. Zoeae rely on armor to protect them from attack rather than evasion. Zoeae rarely attempted to evade attacks, but occasionally attempted to escape following an attack.

Spines are effective at preventing predation by two species of fishes with very different feeding modes. Thus, spines may serve as an effective antipredatory adaptation against the young of most species of fishes, which are among the likeliest predators of estuarine crab zoea. The abundance of young fishes is greatest during the reproductive season of crabs in the shallow, low salinity marshes of the upper estuary where the larvae of R. harrisii develop (Cain and Dean, 1976; Crabtree and Dean, 1979; Weinstein, 1979; Boesch and Turner, 1984). In fact, spines were demonstrated in this study to be effective against the two fishes which predominate in upper estuaries of the east coast of the United States (Richards and Castagna, 1970; McErlean et al., 1972; Subrahmanyam and Drake, 1975; Hillman et al., 1976).

Selection for Spines in Freshwater Versus Marine Plankers

Spines of freshwater zooplankters have repeatedly been shown to be effective at deterring invertebrate predation.

Rotifers produce elongate spines and cladocerans form helmets and long tail spines during summer when predation intensifies. Helmets and spines increase the hydrodynamic efficiency of cladocerans, and thereby increase the evasive capabilities of the organism (O'Brien and Vinyard, 1978; Grant and Bayly, 1981; Barry and Bayly, 1985; Mort, 1986). However, once captured, helmets (especially those equipped with a horn; Kreuger and Dodson, 1981; Havel and Dodson, 1984), and tough, inflexible carapaces (Kerfoot et al., 1980; Williamson, 1983; Dodson, 1984; Havel, 1985) often increase the probability of escaping the grasp of invertebrate predators while they are manipulating their prey. Some rotifers do not evade attacks by invertebrate predators, but instead rely entirely on spines and a rigid lorica to escape once attacked (Szlauer, 1965; Gilbert and Williamson, 1979; Gilbert and Stemberger, 1984). Rotifers which do not bear spines or armor rely solely on superior evasive maneuvers, but once captured are usually ingested (Gilbert and Williamson, 1979). By contrast, armored rotifers and cladocerans frequently survive once captured (Murtaugh, 1981; Kerfoot, 1977a; Gilbert and Williamson, 1979).

Although the helmets and spines of cladocerans deter predation by copepods, notonectids, midge larvae, and mysids, they are ineffective against fishes (Dodson, 1974; Kerfoot, 1977a; Kerfoot et al., 1980; Murtaugh, 1981; Zaret, 1980b; O'Brien, 1979; O'Brien et al., 1980; Bohl, 1982).

Kerfoot (1977a) implicated fish fry in the removal of large, long-spined cladocerans from the vegetated littoral zone of a lake, permitting the return of small, fecund, nonexuberant forms in shoal waters. Many other field and laboratory studies have documented that fishes prefer large cladocerans to smaller plankters (Zaret, 1980a). Furthermore, O'Brien et al. (1980) determined that helmets increase the size of cladocerans so that they are more difficult for invertebrates to manipulate without altering their susceptibility to fish predation. Only Jacobs (1966 cited in O'Brien and Vinyard, 1978) has reported that helmeted forms suffer less predation by fishes than nonhelmeted forms, although he did not identify whether helmets increased their evasive capabilities or made them more difficult to swallow. The ability of the spines of rotifers to deter fish predation apparently remains unexamined.

In contrast, the spines of crab zoeae are far more effective at deterring predation by fishes than invertebrates, despite the similarity in the mode of operation to those of rotifers and cladocerans. Like rotifers and cladocerans, zoeae primarily rely on their armor for protection. Once attacked, zoeae and rotifers flare their spines. Rotifers can become lodged temporarily in the pharynx of the predatory rotifer, and zoeae may become wedged permanently in the pharynx of the fish resulting in its death. The sharp spines of rotifers and zoeae also can irritate the lining of the pharynx. Rejected zoeae and

rotifers passively sink with their spines flared, as do cladocerans with their fixed spines. Zoeae and rotifers collapse their spines shortly after an attack and resume swimming.

If the behavior of zooplankters bearing spines, and the mode of operation of the spines themselves, show so many similarities, then why are spines primarily effective against invertebrates in freshwaters and fishes in marine systems? The answer lies in differences in the size and diversity of invertebrate predators, the abundance of fish larvae, and plankter morphology occurring in the two systems.

First, all predators employed in this study were sufficiently large to prey on zoeae regardless of the presence of spines, except one of the smallest predators, E. mira. However, freshwater invertebrate predators are all relatively small in comparison to their zooplankton prey, and a slight increase in the size of the prey provided by helmets or longer spines is effective at deterring predation.

Second, the greater diversity of marine invertebrates with their variety of feeding modes may account partially for the differential effectiveness of spines against invertebrate predators in marine and freshwaters. Third, important planktivores in freshwaters appear to be unimportant in marine waters. Of the predominant invertebrate planktivores in freshwaters, copepods, rotifers, cladocer-

ans, notonectids, aquatic insect larvae, and mysids, only mysids and the predaceous copepods, Animalocera and Labidocera, are abundant in marine waters. Furthermore, predaceous copepods and mysids simply may be too small to prey upon zoeae. Although zoeae have not been reported as occurring in the diets of mysids (Fulton, 1982), it is still conceivable that removal of zoeal spines would render the zoeae vulnerable to predation by mysids. Predaceous copepods are capable of preying on soft-bodied fish larvae (Lillelund and Lasker, 1974; Turner et al., 1985), although it is unknown if they are large enough to handle the armor of zoeae.

Fourth, the multiple spines of crab zoeae are more effective at deterring fish predation than the single spine and helmet of freshwater cladocerans. The combination of the increase in size with the noxious attributes of spines extending in all directions preclude the possibility of manipulating the zoea so it can be swallowed easily and painlessly. Although freshwater rotifers bear multiple spines their small body size precludes them from occurring in the diets of all but the smallest fish larvae.

Fifth, the spines of freshwater zooplankters may deter predation by young fishes as they do in marine systems, even though they are ineffective against juvenile and adult fishes. Bluegill fry in lakes select Bosimina spp. and avoid Daphnia spp. (Werner, 1969; Siefert, 1972; Beard, 1982) However, despite the considerable attention devoted

to predation in freshwaters, the effectiveness of spines of freshwater zooplankters against larval and postlarval fishes apparently has not been determined.

# LITERATURE CITED

Alvarino, A. 1980. The relation between the distribution of zooplankton predators and anchovy larvae. Cal. Coop. Oceanic Fish. Invest. 21: 150-160.

Barry, M. J. and I. A. E. Bayly. 1985. Further studies on predator induction of crests in Australian Daphnia and the effects of crests on predation. Aust. J. Mar. Freshw. Res. 36: 519-535.

Bayliff, W. H., Jr. 1950. The life history of the silverside Menidia menidia (Linnaeus). Md. Bd. Nat. Res. 90: 1-25.

Beard, T. D. 1982. Population dynamics of young-of-the-year bluegill. Wisconsin Dep. Nat. Res., Tech. Bull. 127: 1-32.

Boesch, D. F. and R. E. Turner. 1984. Dependence of fishery species on salt marshes: the role of food and refuge. Estuaries 7: 460-468.

Bohl, E. 1982. Food supply and prey selection in planktivorous Cyprinidae. Oecologia 134-138.

Breck, J. E. and M. J. Gitter. 1983. Effect of fish size on the reactive distance of bluegill (Lepomis macrochirus) sunfish. Can. J. Fish. Aquat. Sci. 40: 162-167.

Bronmark, C., B. Malmqvist and C. Otto. 1984. Anti-predator adaptations in a neustonic insect. Oecologia 61: 189-191.

Burrell, V. G., Jr. and Van Engel, W. A. 1976. Predation by and distribution of a ctenophore, Mnemiopsis leidyi A. Agassiz, in the York River estuary. Estuar. Coast. Mar.

Sci. 4: 235-242.

Cain, R. L. and J. M. Dean. 1976. Annual occurrence, abundance and diversity of fish in a South Carolina intertidal creek. Mar. Biol. 36: 369-379.

Checkley, D. M., Jr. 1982. Selective feeding by Atlantic herring (Clupea harengus) larvae on zooplankton in natural assemblages. 9: 245-253.

Confer, J. L. and P. I. Blades. 1975. Omnivorous zooplankton and planktivorous fish. Limnol. Oceanogr. 20: 571-579.

Costlow, J. D., Jr., C. G. Bookhout and R. Monroe. 1966. Studies on the larval development of the crab, Rhithropanopeus harrisii (Gould). 1. The effect of salinity and temperature on larval development. Physiol. Zool. 39: 81-100.

Cowden, C., C. M. Young and F. S. Chia. 1984. Differential predation on marine invertebrate larvae by two benthic predators. Mar. Ecol. Progr. Ser. 14: 145-149.

Crabtree, R. E. and J. M. Dean. 1982. The sturcture of two South Carolina estuarine tide pool fish assemblages. Estuaries 5: 2-9.

Cronin, L. E., J. C. Daiber and E. M. Hulbert. 1962. Quantitative seasonal aspects of zooplankton in the Delaware River estuary. Chesapeake Science 3: 63-93.

Dill, L. M. 1983. Adaptive flexibility in the foraging behavior of fishes. Can. J. Fish. Aquat. Sci. 40: 398-408.

Dodson, S. I. 1974. Adaptive change in plankton morphology

in response to size-selective predation: a new hypothesis of cyclomorphosis. Limnol. Oceanogr. 19: 721-729.

Dodson, S. I. 1984. Predation of Heterocope septentrionalis on two species of Daphnia: morphological defenses and their cost. Ecology 65: 1249-1257.

Drenner, R. W., J. R. Strickler and W. J. O'Brien. 1978. Capture probability: the role of zooplankter escape in the selective feeding of planktivorous fish. J. Fish. Res. Bd. Canada 34: 1370-1373.

Durbin, A. G. 1979. Food selection by plankton feeding fishes. In: Clepper, M. (ed.), International Symposium on Predator-Prey Systems in Fish Communities and Their Role in Fisheries Management. Atlanta, Georgia, July 24-27, 1978. Sport Fishing Institute, Washington, D. C., 4: 203-218.

Fisher, D. C. 1977. Functional significance of spines in the Pennsylvanian horseshoe crab Euproops danae. Paleobiol. 3: 175-195.

Freeman, J. A. 1983. Spine regeneration in larvae of the crab, Rhithropanopeus harrisii. J. Exp. Zool. 225: 443-448.

Fulton, R. S., III. 1982. Predatory feeding of two marine mysids. Mar. Biol. 72: 183-191.

Gilbert, J. J. 1967. Asplanchna and postero lateral spine production in Brachionus calyciflorus. Arch. Hydrobiol. 64: 1-62.

Gilbert, J. J. and R. S. Stemberger. 1984. Asplanchna-indu-

ced polymorphism in the rotifer Keratella slacki. Limnol. Oceanogr. 29: 1309-1316.

Gilbert, J. J. and C. E. Williamson. 1978. Predator-prey behavior and its effect on rotifer survival in associations of Mesocyclops edax, Asplanchna girodi, Polyarthra vulgaris, and Keratella cochlearis. Oecologia 37: 13-22.

Gould, S. J. and R. C. Lewontin. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc. Roy. Soc. Lond. B 205: 581-598.

Govoni, J. J., P. B. Ortner, R. Al-Yamani and L. C. Hill. 1986. Selective feeding of spot, Leiostomous xanthurus, and Atlantic croaker, Micropogonias undulatus, larvae in the northern Gulf of Mexico. Mar. Ecol. Prog. Ser. 28: 175-183.

Grant, J. W. G. and I. A. E. Bayly. 1981. Predator induction of crests in morphs of the Daphnia carinata King complex. Limnol. Oceanogr. 26: 201-218.

Hairston, N. G., Jr. and S. S. Easter. 1982. Fish vision and the detection of planktonic prey. Science 218: 1240-1242.

Hardy, A. 1956. the Open Sea: Its Natural History. Houghton Mifflin col., Boston. 322 pp.

Havel, J. E. 1985. Predation of common invertebrate predators on long- and short-featured Daphnia retrocurva. Hydrobiologia 124: 141-149.

Havel, J. E. and S. I. Dodson. 1984. Chaoborus predation on typical and spined morphs of Daphnia pulex: behavioral observations. Limnol. Oceanogr. 29: 487-494.

Hessen, D. O. 1985. Selective zooplankton predation by pre-adult roach (Rutilus rutilus): the size-selective hypothesis versus the visibility-selective hypothesis. Hydrobiologia 124: 73-79.

Hillman, R. E., N. W. Davis, and J. Wennemer. 1977. Abundance, diversity, and stability in shore-zone fish communities in an area of Long Island Sond affected by the thermal discharge of a nuclear power station. Estuar. Coast. Mar. Sci. 5: 355-381.

Hoogland, R. D. Morris and N. Tinbergen. 1957. The spines of sticklebacks (Gasterosteus and Pygosteus) as means of defense against predators (Perca and Esox). Behaviour 10: 205-236.

Hunter, J. R. 1980. The feeding behavior and ecology of marine fish larvae. In: J. E. Bardach (ed.) The Physiological and Behavioral Manipulation of Food Fish as Production and Management Tools, pp. 287-330.

Hutchinson, G. E. 1967. A Treatise on Limnology: Introduction to Lake Biology and the Limnoplankton. Vol. 2, NY, Wiley.

Jacobs, J. 1966. Predation and rate of evolution in cyclomorphotic Daphnia. Int. Ver. Theor. Angew. Limnol. Verh. 16: 1645-1652.

Jacobs, J. 1967. Untersuchen zuer funktion and evolution der

zyklomorphkose bei Daphnia, mit besonderer berucksichtigung der selektion durch fische. Arch. Hydrobiol. 62: 467-541.

Kerfoot, W. C. 1977a. Implications of copepod predation. Limnol. Oceanogr. 22: 316-325.

Kerfoot, W. C. 1977b. Competition in cladoceran communities: the cost of evolving defenses against copepod predation. Ecology 58: 303-313.

Kerfoot, W. C., D. L. Kellogg, Jr. and J. R. Strickler. 1980. Visual observations of live zooplankters: evasion, escape, and chemical defenses. In: Evolution and Ecology of Zooplankton Communities. Kerfoot, W. C. (ed.)., University Press of New England, Hanover, pp. 10-27.

Kneib, R. T., and A. E. Stiven. 1978. Growth, reproduction, and feeding of Fundulus heteroclitus (L.) on a North Carolina salt marsh. J. Exp. Mar. Biol. Ecol. 31: 121-140.

Kreuger, D. A. and S. I. Dodson. Embryological induction and predation ecology in Daphnia pulex. Limnol. Oceanogr. 26: 219-223.

Lebour, M. V. 1919. The feeding habits of some young fish. J. Mar. Biol. Assoc. U. K. 12: 9-21.

Li, K. T., J. K. Wetterer and N. G. Hairston, Jr. 1985. Fish size, visual resolution, and prey selectivity. Ecology 66: 1729-1735.

Lillelund, K. and R. Lasker. 1971. Laboratory studies of

predation by marine copepods on fish larvae. Fish. Bull. 69: 655-667.

Lindstrom, T. 1955. On the relation fish-size, food-size. Rept. Inst. Freshwater Res., Drottingholm 36: 133-147.

Lough, R. G. 1976. Larval dynamics of the dungeness crab, Cancer magister, off the central Oregon coast, 1970--1971. Fish. Bull. 74: 352-374.

Magnahagen, C. 1985. Random prey capture or active choice? An experimental study on prey size selection in three marine fish species. Oikos 45; 206-216.

Magnahagen, C. and A.-M. Wiederholm. 1982. Food selectivity versus prey availabiltiy: a study using the marine fish Pomatoschistus microps. Oecologia 55: 311-315.

Marak, R. R. 1974. Food and feeding of larval redfish in the Gulf of Maine. In: The Early Life History of Fish. J. H. S. Blaxter (ed.), Springer-Verlag, NY.

McErlean, A. J., S. G. O'Conner, J. A. MLihursky and C. I. Gibson. 1972. Abundance, diversity and seasonal patterns of estuarine fish populations. Estuar. Coastal Mar. Sci. 1: 19-36.

Middaugh, D. P. 1981. Reproductive ecology and spawning periodicity of the Atlantic silverside, Menidia menidia (Pisces: Atherinidae). Copeia 1981: 766-776.

Mileikovsky, S. A. 1974. On predation of pelagic larvae and early juveniles of marine bottom invertebrates by adult benthic invertebrates and their passing alive through their predators. Mar. Biol. 26: 303-311.

Mort, M. A. 1986. Chaoborus predation and the function of phenotypic variation in Daphnia. Hydrobiologia 133: 39-44.

Mulkana, M. S. 1966. The growth and feeding habits of juvenile fishes in two Rhode Island estuaries. Gulf Res. Rep. 2: 97-168.

Murtaugh, P. A. 1981. Inferring properties of mysid predation from injuries to Daphnia. Limnol. Oceanogr. 26: 811-821.

Neave, D. A. 1984. The development of visual acuity in larval plaice (Pleuronectes platessa L.) and turbot (Scopthalmus maximus L.). J. Exp. Mar. Biol. Ecol. 78: 167-175.

O'Brien, W. J. 1979. The predator-prey interaction of planktivorous fish and zooplankton. Amer. Sci. 67: 572-581.

O'Brien, W. J., D. Kettle, and H. Riessen. 1979. Helmets and invisible armor: structures reducing preation from tactile and visual planktivores. Ecology 60: 287-294.

O'Brien, W. J., D. Kettle, H. Riessen, D. Schmidt and D. Wright. 1980. Dimorphic Daphnia longiremis: predation and competitive interactions between the two morphs. In: Ecology and Evolution of Zooplankton Communities. Kerfoot, W. C. (ed.), University Press of New England, Hanover, pp. 497-506.

O'Brien, W. J. and G. L. Vinyard. 1978. Polymorphism and predation: the effect of invertebrate predation on the

distribution of two varieties of Daphnia carinata in South India ponds. Limnol. Oceanogr. 23: 452-460.

Pennington, J. T. and F.-S. Chia. 1984. Morphological and behavioral defenses of trochophore larvae of Sabellaria cementarium (Polychaeta) against four planktonic predators. Biol. Bull. 167: 168-175.

Peterson, W. T. and S. J. Ausubel. 1984. Diets and selective feeding by larvae of Atlantic mackerel Scomber scombrus on zooplankton. Mar. Ecol. Prog. Ser. 17: 65-75.

Reynolds, J. G. and M. C. Geddes. 1984. Functional response analysis of size-selective predation by the notonectid predator Anisops deanei (Brooks) on Daphnia thomsoni (Sars). Aust. J. Mar. Freshw. Res. 35: 725-733.

Richards, C. E. and M. Castagna. 1970. Marine fishes of Virginia's eastern (shore inlet and marsh, seaside waters). Chesapeake Sci. 11: 235-248.

Riessen, H. P. 1984. The other side of cyclomorphosis: why Daphnia lose their helmets. Limnol. Oceanogr. 29: 1123-1127.

Siefert, R. 1972. First food of larval yellow perch, white sucker, bluegill, emerald shiner and rainbow smelt. Trans. Am. Fish. Soc. 101: 219-225.

Strathmann, R. R. 1981. The role of spines in preventing structural damage to echinoid tests. Palaeobiol. 7: 407-411.

Subrahmanyam, C. B. and S. H. Drake. 1975. Studies on the animal communities in two north Florida salt marshes.

Bull. Mar. Sci. 25: 445-465.

Szlauer, L. 1965. The refuge ability of plankton animals before plankton eating animals. Pol. Arch. Hydrobiol. 13: 89-95.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. 25: 1-45.

Turner, J. T., P. A. Tester and W. F. Hettler. 1985. Zooplankton feeding ecology: a laboratory study of predation on fish eggs and larvae by the copepods Anomalocera ornata and Centropages typicus. Mar. Biol. 90: 1-8.

Unger, P. A. and W. M. Lewis, Jr. 1983. Selective predation with respect to body size in a population of the fish Xenomelaniris veneauelae (Atherinidae). Ecology 64: 1136-1144.

Vermeij, G. J. 1982. Unsuccessful predation and evolution. Amer. Natur. 120: 701-720.

Vinyard, G. L. 1980. Differential prey vulnerability and predator selectivity: effects of evasive prey on bluegill (Lepomis macrochirus) and pumpkinseed (L. gibbosus) predation. Can. J. Fish. Aquat. Sci. 37: 2294-2299.

Ware, D. M. 1972. Predation by rainbow trout (Salmo gaidneri): the influence of hunger, prey density, and prey size. J. Fish. Res. Bd., Canada 29: 1193-1201.

Weldon, W. F. R. 1889. Notes on the function of the spine of the crustacean zoeae. J. Mar. Biol. Assoc. U.K. 1:

169-171.

Weinstein, M. P. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. Fish. Bull. 77: 339-356.

Werner, E. E. 1974. The fish size, prey size, handling time relation in several sunfishes, and some implications. J. Fish. Res. Bd. Canada 31: 1531-1536.

Werner, E. E., G. G. Mittelbach and D. J. Hall. 1981. The role of foraging profitability and experience in habitat use by the bluegill sunfish. Ecology 62: 116-125.

Werner, R. G. 1969. Ecology of limnetic bluegill (Lepomis macrochirus) fry in Crane Lake, Indiana. Am. Midl. Nat. 81: 164-181.

Williams, G. C. 1966. Adaptation and natural selection: a critique of some current evolutionary thought. Princeton University Press, Princeton, 307 pp.

Williamson, C. E. 1983. Behavioral interactions between a cyclopoid copepod predator and its prey. J. Plankton Res. 5: 701-711.

Zaret, T. M. 1980a. Predation and freshwater communities. Yale University Press, New Haven, 187 pp.

Zaret, T. M. 1980b. The effect of prey motion on planktivore choice. Symp. Amer. Soc. Limnol. Oceanogr. 3; 594-603.

Zaret, T. M. and J. S. Suffern. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. Limnol. Oceanog. 21: 804-813.

# CHAPTER 3

# MORPHOLOGICAL AND BEHAVIORAL ANTIPREDATORY ADAPTATIONS OF DECAPOD ZOEAE

## ABSTRACT

Zoeae of some species of estuarine decapods are retained in the estuary throughout development while others are exported into nearshore coastal waters. The horizontal migrations of decapod zoeae to coastal waters may have evolved to reduce the probability of encountering planktivorous fishes which are most abundant in the estuary. If so, then the morphological vulnerability of zoeae to fish predation should be inversely related to the number of predators occurring where they develop. Six species of estuarine decapod zoeae were offered to Menidia menidia and Fundulus heteroclitus. The behavioral interactions were observed to determine the prey's vulnerability to predation, and the mode of operation and relative effectiveness of their defenses. Feeding trials and behavioral observations both demonstrated that M. menidia 6-16 mm long preferred Uca minax and Callinectes sapidus zoeae, which are exported from the estuary, to Rhithropanopeus harrisii, Sesarma reticulatum and Palaemonetes pugio, which are retained within estuaries. Pinnotheres ostreum zoeae develop in the lower estuary and fish demonstrated an intermediate preference for the zoeae. Menidia menidia 20-40 mm long showed the same preferences for R. harrisii, S. reticulatum, P. ostreum and S. reticulatum as did small silversides. Large-mouthed demersal fish, Fundulus heteroclitus 6-10 mm long, also preferred U. minax to R. harrisii, but more readily preyed on zoeae than did M. menidia. The

exported species of zoeae have shorter spines and smaller bodies than do retained zoeae, except P. ostreum which is small, spineless and passively sinks when attacked by fish. Other retained species of zoeae also have postcontact behavioral defenses which enhance the effectiveness of their morphological defenses. Zoeae do not evade attacks by fishes, but fishes quickly learned to avoid zoeae, which increases the effectiveness of the zoeae's antipredatory adaptations.

# INTRODUCTION

Zooplankters have long been known to undergo diurnal vertical migrations, but it is not widely recognized that they also make extensive horizontal migrations. Existing evidence best supports the hypothesis that vertical migrations are undertaken to reduce the probability of encountering zooplanktivorous fishes in illuminated waters (Zaret and Suffern, 1976; Stitch and Lampert, 1981; Gliwicz, 1986). Horizontal migrations of estuarine crab zoeae to coastal waters may also have evolved to avoid fish predation, because fishes are most abundant in estuaries during the summer when crabs hatch (McErlean et al., 1972; Cain and Dean, 1976; Subrahmanyam and Drake, 1975; Weinstein, 1979; Crabtree and Dean, 1982). The silverside, Menidia menidia, the anchovy, Anchoa mitchelli, and the killifish, Fundulus heteroclitus, are the predominant fishes in the upper estuary where many crabs reside (Richards and Castagna, 1970; Derickson and Price, 1973; Targett and McCleave, 1974; Cain and Dean, 1976). Silversides and anchovies eat plankton as adults (Bengston, 1984; Smith et al., 1984), and all fish larvae are planktivorous (Hunter, 1980; Turner, 1984). Larval and juvenile fishes are particularly abundant in low salinity marshes (Cain and Dean, 1976; Weinstein, 1979), and the great abundance of young fishes can have a considerable impact on estuarine zooplankton communities (Thayer et al., 1974; Bengston, 1984). Thus, predation on larval populations of invertebrates may be great in the

upper estuary.

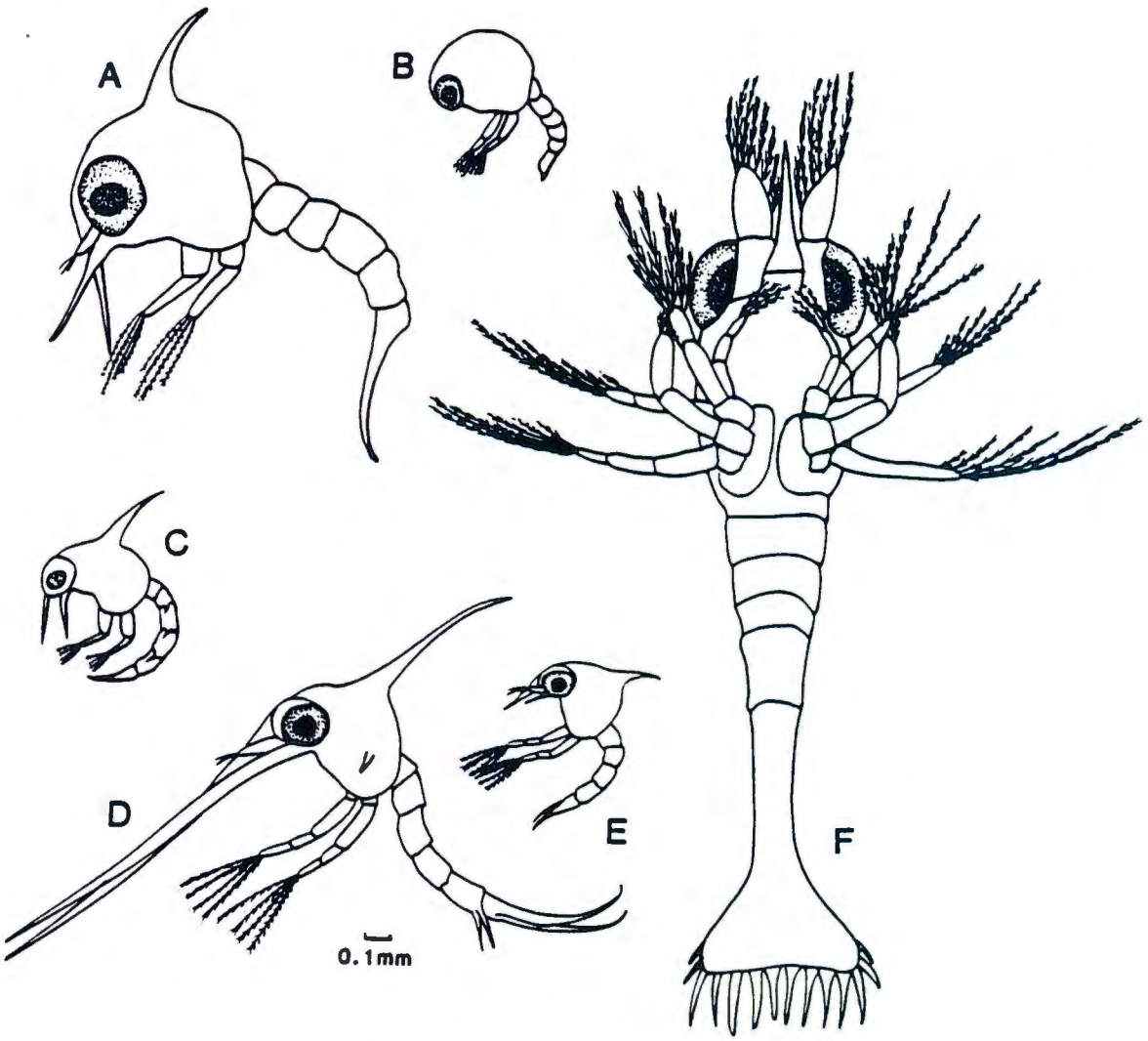
Therefore larvae that are hatched and retained in the upper estuary should encounter the greatest risk of fish predation, and should have evolved very effective morphological or behavioral antipredatory adaptations. The mud crab, Rhithtropanopeus harrisii, the marsh crab, Sesarma reticulatum, and the grass shrimp, Palaemonetes pugio, hatch and develop in the upper estuary (Pinschmidt, 1963; Sandifer, 1973; Cronin, 1982), and should have the best defenses against fish predation. The fiddler crab, Uca minax, also hatches in the upper estuary, but its zoeae are quickly transported from the estuary. Blue crabs migrate to the lower estuary to release their zoeae which are carried 80 km offshore (Smyth, 1980; Provenzano et al., 1983; Truesdale and Andryszak, 1983; Millikin and Williams, 1984). These zoeae may be exported from the estuary into safer coastal waters because they are morphologically susceptible to fish predation. The pea crab, Pinnotheres ostreum hatches primarily in the middle or lower estuary (Flower and McDermott, 1952), and zoeae develop near the mouth of the estuary (Sandifer, 1973; Goy, 1976). Thus, pea crab zoeae may have better defenses against fish predation than would be expected for fiddler or blue crab zoeae, but less effective antipredatory adaptations than mud crab, shore crab or grass shrimp zoeae.

The most prominent trait of decapod zoeae that could serve as a defense against predators is their spines.

Morgan (1987) demonstrated that spines increase the size of mud crab zoeae, and thereby reduce predation by small fishes. Consequently, the largest zoeae, including body size and spine length, should be least vulnerable to predation by small fishes. Grass shrimp zoeae are the largest of the six species of zoeae (Figure 1), but bear only one short rostral spine. Among the crab zoeae, mud crabs have the greatest total size, followed by the marsh crab. Blue crab, fiddler crab and pea crab zoeae are small and should be most preferred by fishes. Pea crab zoeae are spineless, and should be preyed upon most frequently, provided that they rely solely on morphological traits to deter fish predation. However, behavioral antipredatory adaptations may also influence the preferences of fishes for the various zoeae.

Thus, I have subjected the six species of estuarine decapod zoeae to predation by two species of fishes with different feeding modes to determine their vulnerability to predation, and the mode of operation and relative effectiveness of their defenses. If predation enforces selection for defense mechanisms, the vulnerability of zoeae should be inversely related to the number of predators occurring where they develop. Zoeae with the best defenses should be those retained in the upper estuary where planktivorous fishes abound. Zoeae which quickly disperse to coastal waters where fishes are less abundant should be most vulnerable to predation.

Figure 1. First instar zoeae of A) *Sesarma reticulatum*, B) *Pinnotheres ostreum*, C) *Callinectes sapidus*, D) *Rhithropanopeus harrisii*, E) *Uca minax* and F) *Palaemonetes pugio* drawn to comparable scale.


A
B
C
D
E
F
0.1mm

# METHODS AND MATERIALS

## Selection of Experimental Organisms

Six common species of decapod zoeae were fed to predators: R. harrisii, P. ostreum, U. minax, C. sapidus, S. reticulatum, and P. pugio (Figure 1). The larvae of all species hatch from April to September in the Newport and Neuse River estuaries, North Carolina, where the study was conducted. The six species of decapod zoeae vary in spine length and number as well as body size.

Decapod larvae were fed to two fish predators: the Atlantic silverside, Menidia menidia, and the striped killifish, Fundulus heteroclitus. Silversides are selective diurnal planktivores occurring primarily in open waters, ranging from 0-36 o/oo (Bayliff, 1950; Myers, 1976). The killifish feeds opportunistically on a variety of prey, including armored prey (Kneib and Stiven, 1978), and occurs throughout the estuary (Weinstein, 1979). Thus, both of these wide-ranging predators should encounter the six species of decapod larvae in the estuary during the breeding season of the crabs. Furthermore, fishes hatch and develop in the estuary during spring and summer when crabs do (Kneib and Stiven, 1978; Middaugh, 1981), so that zoeae would be subject to larval fish predation.

## General Methodology and Experimental Design

Gravid R. harrisii were collected by using traps that lure crabs to oyster shells provided within. Gravid S. reticulatum and U. minax are semiterrestrial and were

collected by digging up their burrows at low tide. Callinectes sapidus were collected in crab pots or by dipnetting at night while using a light to attract the crabs. Pinnotheres ostreum were obtained by opening oysters collected from intertidal oyster bars. Ovigerous P. pugio and F. heteroclitus were collected with a 15 ft seine in tidal creeks at low tide. Gravid M. menidia were collected with a 50 ft seine in high salinity marshes at low tide.

Eggs of crabs and fishes were hatched in the laboratory and reared under a 12 h light: 12 h dark photoperiod. Decapods were hatched at 25$^{o}$C and from 20-30 o/oo depending on the species. Fishes were hatched at ambient temperatures and salinities in flowing seawater (approximately 25oC and 28-33 o/oo). Thus, naive predators and prey were used during experiments. Predators and prey were used only once. Larvae were reared on Artermia nauplii. Predators were starved at least one day prior to experimentation, and fish were fed several drops of Artemia nauplii following the conclusion of the feeding trial to determine if they were still hungry. Only actively swimming zoeae displaying normal swimming behavior were used in experiments.

Specific Methodology and Experimental Design

The following experiments were done to determine whether 1) spines physically prevent predation by small size classes of fishes, 2) spine length, body size or total size (spines plus body size) of the six species of zoeae are more likely to prevent predation by small fishes, and 3) large-

mouthed killifish are better able to prey on zoeae than are small-mouthed silversides.

The six species of zoeae were fed separately to silversides in 6 cm bowls for 24 h and the number of surviving larvae was counted. Fish from 6-16 mm standard length in 2 mm size class increments were fed first instar zoeae. Uca minax and R. harrisii also were fed separately to killifish (6, 8, 10 mm SL) in 6 cm bowls. Silversides 20 and 40 mm long were fed R. harrisii, S. reticulatum, P. ostreum, and U. minax zoeae together to determine the vulnerability of zoeae to predation by large fish during a 15 min period.

The behavioral interactions of predator and prey were observed for ten minutes (two consecutive five minute intervals) following the introduction of the zoeae into the bowl with the fish, to determine 1) if antipredatory behavior by zoeae was evident, 2) if fish experienced more difficulty with some zoeae than others, and 3) if fish learned to avoid some zoeae and not others. The behavioral interactions of the fish were quantified using the following categories: attacks, avoidances, captures, mouthing, ingestion, and unusual behavior following capture or ingestion. Unusual behavior indicating that the fish was experiencing difficulty with the prey included shaking the zoeae, shuddering, and sinking while attempting to swallow the zoeae. Zoeal behavior was categorized as evasion before and escape after attack. Orthogonal polynomial contrasts of

behavioral data were analyzed by the analysis of variance.

## RESULTS

Callinectes sapidus, U. minax and P. ostreum zoeae were most susceptible to predation by silversides less than 16 mm long, and R. harrisii and P. pugio were least vulnerable to predation (Figure 2A). Sesarma reticulatum demonstrated an intermediate susceptiblity to predation by small silversides. Small killifish also consumed more U. minax than R. harrisii zoeae (Figure 2B). Large silversides continued to prefer U. minax to R. harrisii zoeae, but preferred S. reticulatum to P. ostreum (Figure 3). Zoeae were consumed increasingly as silversides and killifish increased in length (Figures 2, 3).

A comparison of behavioral interactions between 12 mm silversides (M. menidia) and the six species of zoeae revealed that P. ostreum and U. minax were avoided significantly less often than were other zoeae (Table 1). All species of zoeae were attacked with similar frequency. Pinnotheres ostreum zoeae were captured most often, followed by C. sapidus and U. minax zoeae. Sesarma reticulatum, R. harrisii and P. pugio zoeae were captured least often. Uca minax and C. sapidus zoeae were ingested more often than were other species. Uca minax zoeae also were mouthed more often than other species, and S. reticulatum were shaken less often. All zoeae attempted to evade attacks with similar frequency, but P. pugio most often attempted to escape following attack.

Figure 2. Number of zoeae remaining after 24 h in the presence of A) *M. menidia* 10-12 mm long and B) *F. heteroclitus* 6-10 mm long.

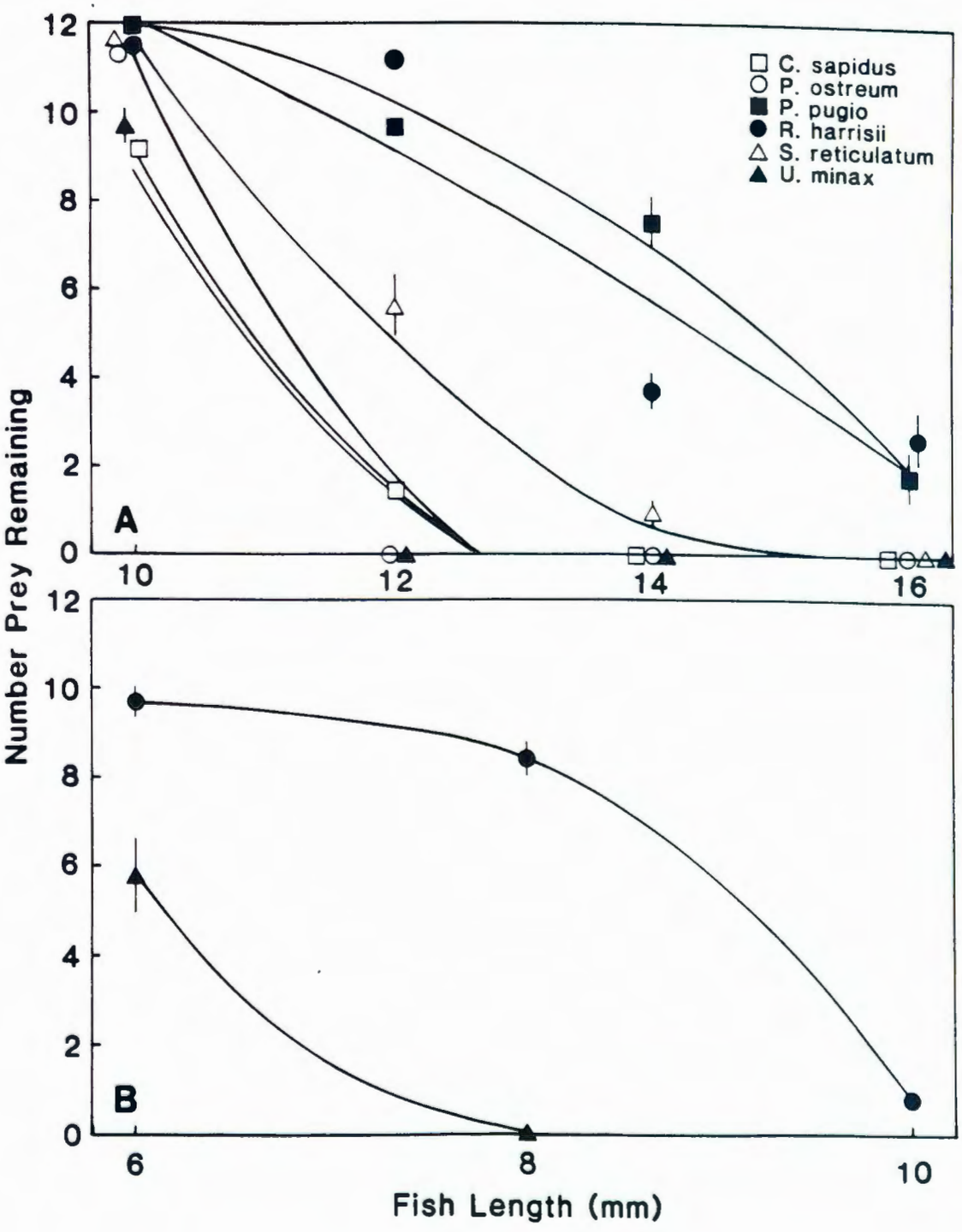

C. sapidus
P. ostreum
P. pugio
R. harrisii
S. reticulatum
U. minax
A
B
Number Prey Remaining
Fish Length (mm)
0
2
4
6
8
10
12
10
12
14
16
6
8
10

Figure 3. Number of zoeae remaining after 15 min in the presence of M. menidia 20 and 40 mm long.

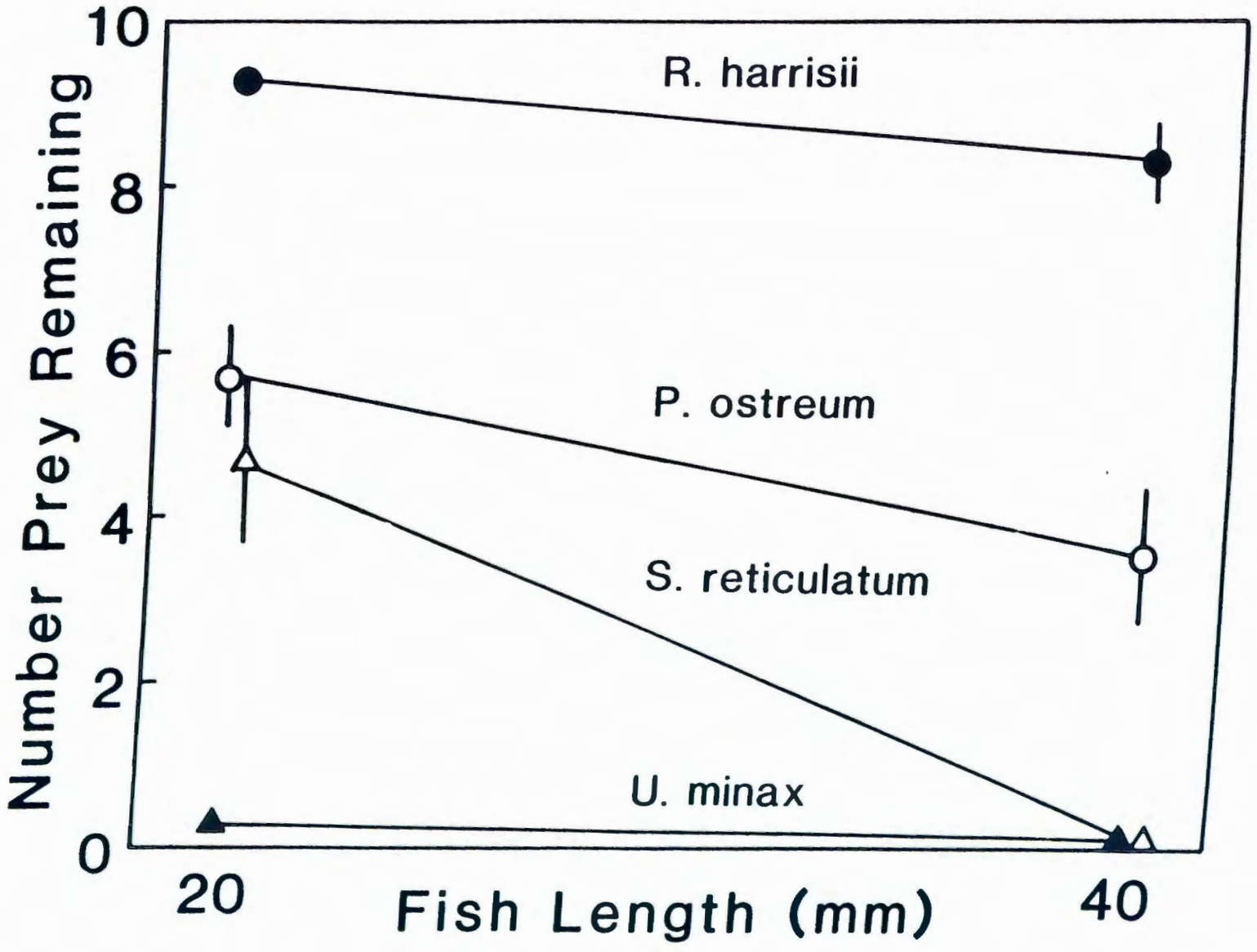

10
8
6
4
2
0
Number Prey Remaining
R. harrisii
P. ostreum
S. reticulatum
U. minax
20
Fish Length (mm)
40

Table 1. Analysis of variance and Student Newman Keuls tests of fish and zoeal interactions between six species of zoeae fed to 12 mm M. menidia, and between R. harrisii and U. minax zoeae fed to 6 and 8 mm F. heteroclitus (Cs=C. sapidus, Po=P. ostreum, Pp=P. pugio, Rh=R. harrisii, Sr=S. reticulatum, and Um=U. minax; df=94; significance levels: *=.05, **=.01, ***=.001).

| BEHAVIOR | M. menidia | | | F. heteroclitus | | |
|---|---|---|---|---|---|---|
| | MS | F | SNK | MS | F | |
| Avoids/Pursuit | 51.56 | 8.82*** | Sr Pp Rh Cs > Po Um | 98.10 | 10.43*** | Rh > Um |
| Attacks/Pursuit | 34.39 | 2.49* | Po Um Rh Pp ≥ Cs Um | 0.23 | 0.01 | |
| Captures/Attack | 186.54 | 30.51*** | Po > Cs Um > Sr Rh Pp | 223.11 | 16.29*** | Rh < Um |
| Ingestions/Capture | 150.40 | 46.82*** | Cs Um > Po Sr Rh Pp | 264.13 | 35.73*** | Rh < Um |
| Mouthings/Capture | 92.47 | 12.60*** | Um > Sr Rh Po Cs Pp | 430.05 | 43.24*** | Rh < Um |
| Shakes/Capture | 29.57 | 5.21*** | Sr > Pp Cs Rh Um Po | 242.43 | 18.40*** | Rh < Um |
| Evasions/Attack | 0.80 | 0.79 | Rh Po Cs Um Sr Pp | 12.37 | 1.74 | |
| Escapes/Attack | 11.05 | 2.97* | Pp > Um Rh Sr ≥ Cs Po | 82.42 | 15.99*** | Rh > Um |

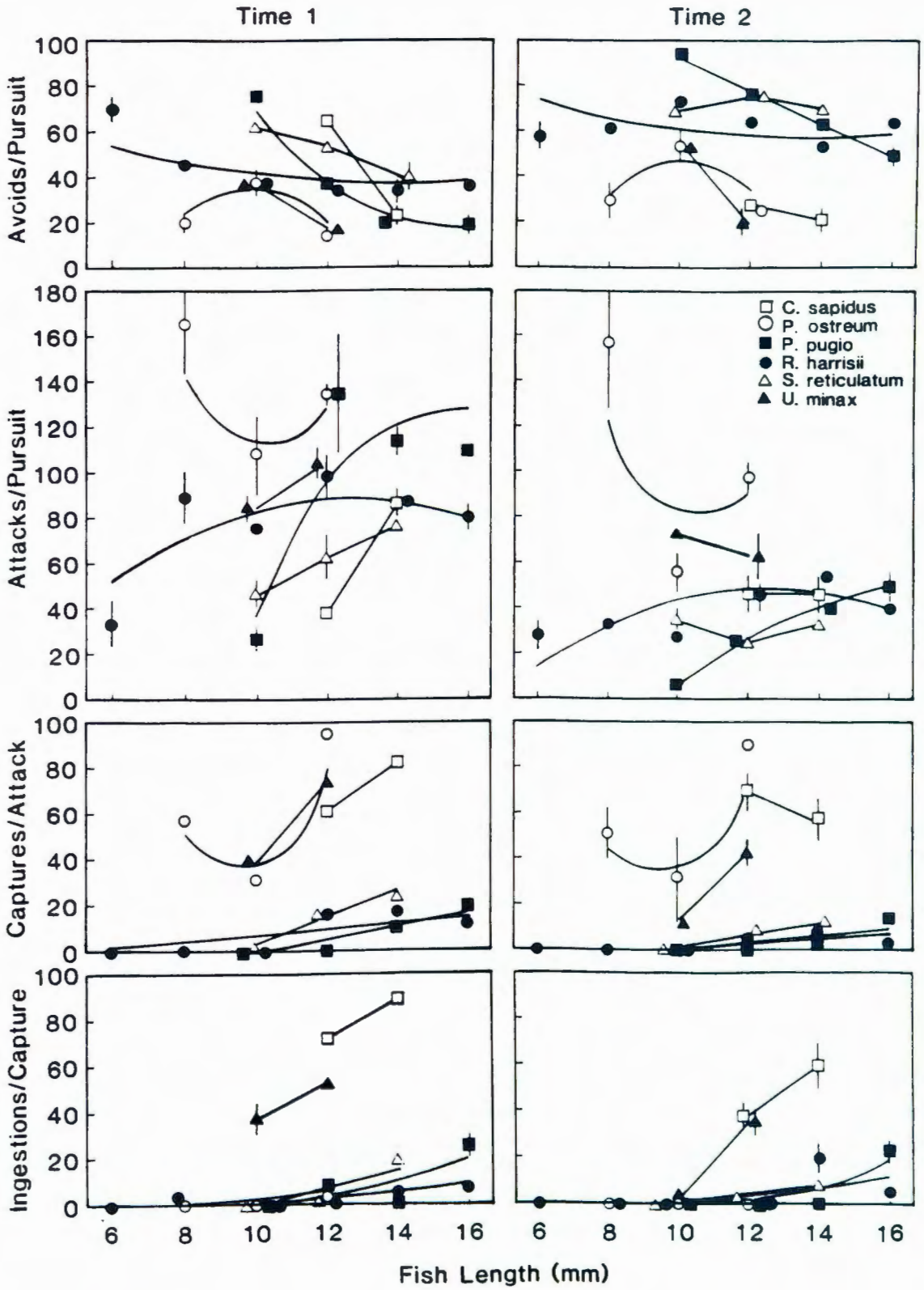
A comparison of interactions between 6-8 mm killifish (F. heteroclitus) and R. harrisii and U. minax zoeae showed that R. harrisii zoeae were avoided more frequently, and captured, mouthed, shaken and ingested less often than U. minax zoeae (Table 1). Rhithropanopeus harrisii zoeae attempted to escape following attack more often than did U. minax zoeae.

Behavioral observations also indicated that large silversides and killifish generally captured, ingested and mouthed P. pugio, R. harrisii, S. reticulatum and U. minax zoeae more often and avoided these zoeae (except S. reticulatum) less frequently than did small fish (Figures 4, 5; Table 2). Only P. pugio and R. harrisii zoeae were attacked more often as fish length increased, and only R. harrisii, S. reticulatum and U. minax zoeae were shaken more frequently.

Silversides and killifish generally avoided P. pugio, R. harrisii, S. reticulatum, and U. minax more as the time of exposure increased, and zoeae were attacked and captured less often (Figure 4, 5; Table 1). Fish mouthed and ingested fewer of these zoeae with time, or their behavior did not change.

The behavior of silversides towards C. sapidus and P. ostreum zoeae generally did not change in a manner that would indicate that large fish were becoming more proficient at handling the zoeae. However, large fish avoided C. sapidus zoeae less than smaller ones, and more P. ostreum

Figure 4. Behavioral interactions between six species of zoeae and *M. menidia* 6-16 mm long during two consecutive five minute observation periods.


Time 1
Time 2
Avoids/Pursuit
Attacks/Pursuit
Captures/Attack
Ingestions/Capture
Fish Length (mm)
C. sapidus
P. ostreum
P. pugio
R. harrisii
S. reticulatum
U. minax

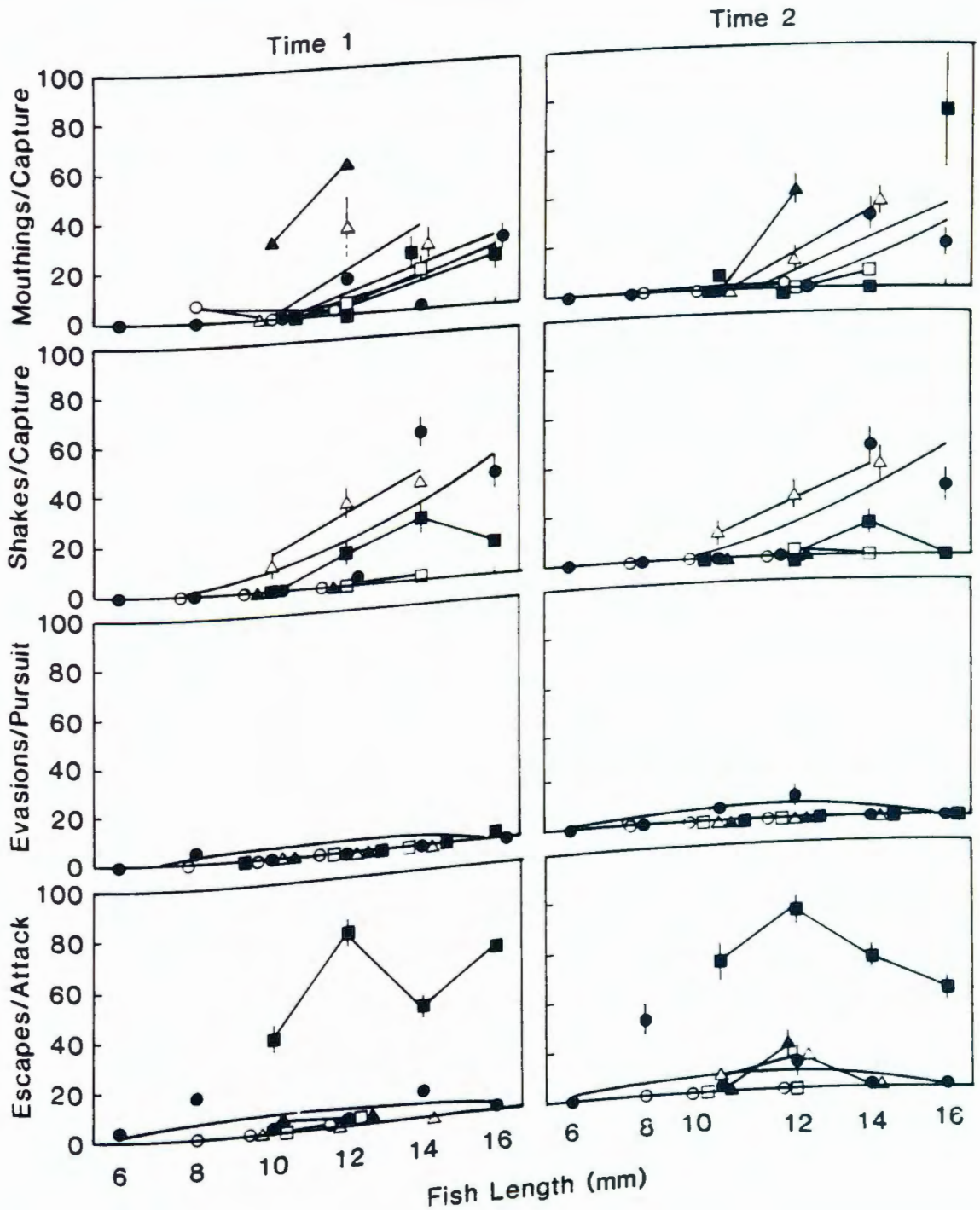

Time 1
Time 2
Mouthings/Capture
Shakes/Capture
Evasions/Pursuit
Escapes/Attack
0
20
40
60
80
100
6
8
10
12
14
16
Fish Length (mm)

Figure 5. Behavioral interactions between R. harrisii and U. minax zoeae and F. heteroclitus 6-10 mm long during two consecutive five minute observation periods.

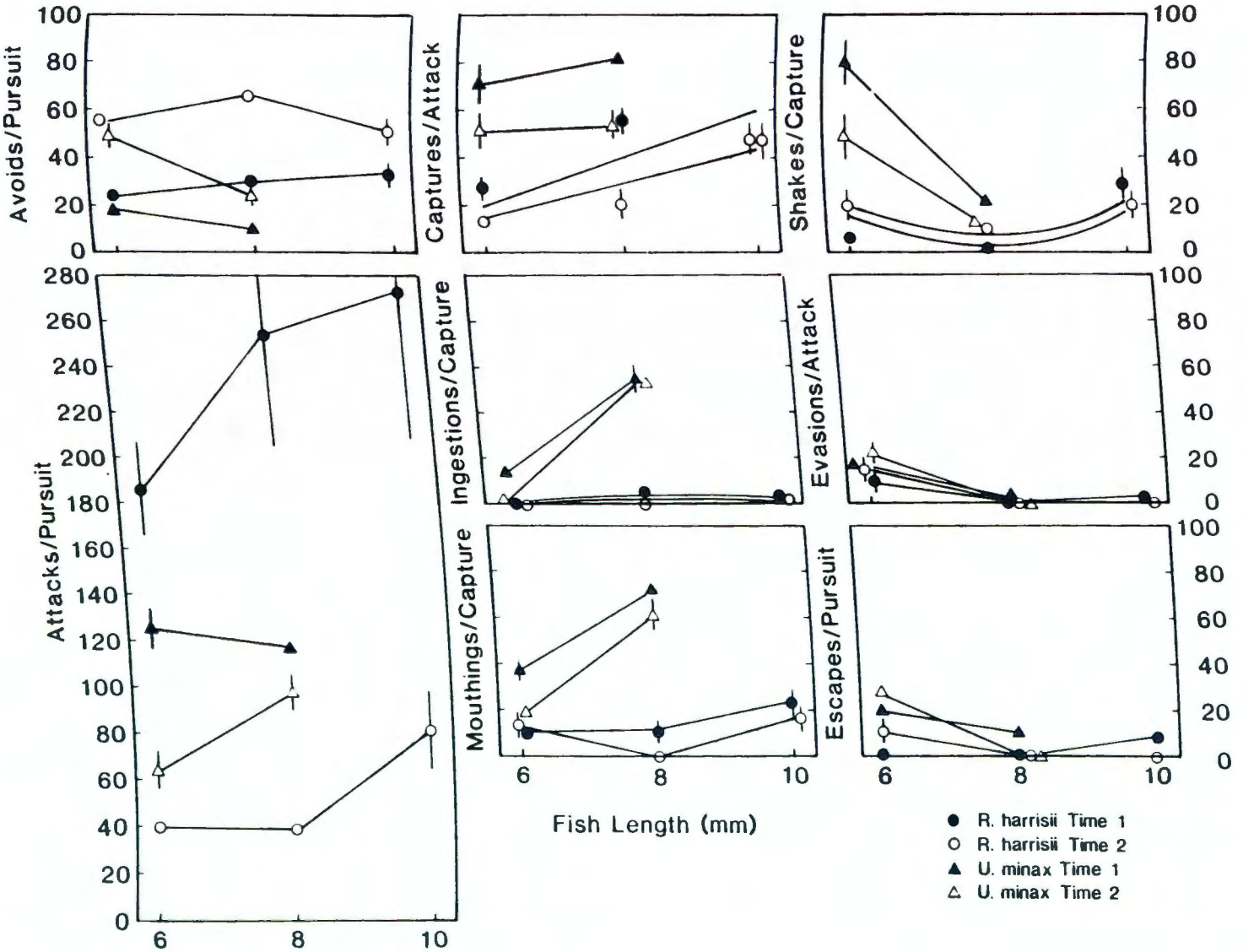

Avoids/Pursuit
Captures/Attack
Shakes/Capture
Attacks/Pursuit
Ingestions/Capture
Evasions/Attack
Mouthings/Capture
Escapes/Pursuit
Fish Length (mm)
R. harrisii Time 1
R. harrisii Time 2
U. minax Time 1
U. minax Time 2

Table 2. Analysis of variance of fish and zoeal behavioral interactions with increasing exposure time and fishlength. Cs=*C. sapidus*, df=23; Po=*P. ostreum*, df=29; Pp=*P. pugio*, df=3,76; Rh=*R. harrisii*; *M. menidia* df=479, *F. heteroclitus* df=57; Sr=*S. reticulatum*, df=59; and Um=*U. minax*: *M. menidia* df=37, *F. heteroclitus* df=39. Sums of squares and significance levels (*=.05, **=.01, ***=.001) are presented. Att=attack, Pur=pursuit, and cap=capture.

| BEHAVIOR | *M. menidia* | | | | | | *F. heteroclitus* | |
|---|---|---|---|---|---|---|---|---|
| | Cs | Po | Pp | Rh | Sr | Um | Rh | Um |
| Avoids/pur | 66.42 | 51.07 | 346.65 | 745.32 | 45.37 | 88.33 | 100.11 | 103.96 |
| Time | 24.95 | 5.19 | 141.85*** | 123.43*** | 39.34** | 3.78 | 70.01** | 57.90* |
| Length | 41.47* | 0.07 | 175.35*** | 588.02*** | 5.62 | 84.55** | 13.58 | 45.06* |
| Length2 | - | 22.22* | 11.21 | 0.20 | 0.42 | - | 12.64 | - |
| T X L2 | - | - | 18.17* | 33.16* | - | - | - | - |
| Error | 151.61 | 142.47 | 270.97 | 3570.93 | 214.35 | 293.54 | 436.78 | 327.89 |
| Attacks/pur | 9.90 | 97.04 | 730.36 | 2108.94 | 92.26 | 74.44 | 147.65 | 80.44 |
| Time | 7.95 | 25.32 | 393.09*** | 703.10*** | 70.55** | 73.58* | 116.20** | 72.33** |
| Length | 1.95 | 7.92 | 247.77*** | 1118.06*** | 20.12 | 0.85 | 2.09 | 8.11 |
| Length2 | - | 63.80* | 89.50** | 184.57*** | 1.58 | - | 3.54 | - |
| T X L2 | - | - | - | 85.28** | - | - | - | - |
| Error | 233.01 | 345.63 | 690.50 | 5627.34 | 442.53 | 551.94 | 537.88 | 336.46 |
| Captures/att | 14.37 | 195.11 | 142.27 | 1798.51 | 152.36 | 213.43 | 151.12 | 86.68 |
| Time | 14.36 | 0.29 | 22.09** | 102.28*** | 28.08** | 121.23*** | 2.53 | 80.07* |
| Length | 0.01 | 78.71* | 119.21*** | 1633.15*** | 117.85*** | 92.19** | 123.69* | 6.61 |
| Length2 | - | 116.11* | 0.91 | 1.93 | 6.43 | - | 11.07 | - |

Table 2. (continued)

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Error | 225.15 | 406.52 | 213.20 | 3021.86 | 134.65 | 284.59 | 760.00 | 407.90 |
| Ingestions/cap | 61.80 | 11.90 | 152.02 | 1512.70 | 75.81 | 203.07 | 278.68 | 247.72 |
| Time | 56.53* | 5.87 | 1.02 | 37.38* | 6.49 | 97.94** | 37.87 | 44.72* |
| Length | 5.27 | 0.15 | 98.50*** | 1370.19*** | 60.36*** | 105.12** | 90.21* | 203.00*** |
| Length2 | - | 2.94* | 52.50*** | 81.89** | 8.97 | - | 147.91** | - |
| T X L2 | - | 2.94* | - | - | - | - | - | - |
| Error | 183.95 | 14.31 | 279.25 | 3922.79 | 175.80 | 344.44 | 715.70 | 274.85 |
| Mouthings/cap | 14.84 | 10.69 | 230.22 | 1940.85 | 188.33 | 289.46 | 272.97 | 172.68 |
| Time | 7.51 | 3.43 | 0.89 | 79.01** | 5.99 | 97.19** | 197.00** | 49.24* |
| Length | 7.32 | 0.60 | 192.15*** | 1806.75*** | 182.27*** | 192.27*** | 25.44 | 123.44* |
| Length2 | - | 6.66* | 37.19 | 25.88 | 0.07 | - | 28.69 | - |
| Error | 109.58 | 23.10 | 781.00 | 6628.76 | 611.27 | 319.90 | 1103.75 | 322.92 |
| Shakes/cap | 0.17 | 0 | 82.66 | 867.29 | 175.57 | 0.68 | 267.75 | 194.47 |
| Time | 0.08 | 0 | 36.47* | 24.21 | 14.54 | 0.32 | 114.28** | 71.95* |
| Length | 0.08 | 0 | 23.53 | 755.00*** | 159.34** | 0.36 | 74.23* | 122.52** |
| Length2 | - | - | 22.67 | 42.93* | 1.68 | - | - | |
| T X L | - | - | - | 37.08* | - | - | - | - |
| Error | 17.76 | 0 | 476.15 | 2140.81 | 799.14 | 11.28 | 786.42 | 519.02 |
| Evasions/att | 0 | 0 | 1.23 | 20.57 | 0 | 0 | 0 | 58.48* |
| Time | 0 | 0 | 0.01 | 2.55 | 0 | 0 | 0 | 0.01 |
| Length | 0 | 0 | 0.02 | 5.01 | 0 | 0 | 0 | 58.47** |
| Length2 | - | - | 1.20 | 11.43* | - | - | - | - |
| Error | 0 | 0 | 46.11 | 1014.15 | 0 | 0 | 0 | 260.53 |

Table 2. (continued)

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Escapes/att | 0 | 0.34 | 81.40 | 37.89 | 18.39 | 34.29 | 1.38 | 66.74 |
| Time | 0 | 0.11 | 3.69 | 0.19 | 4.87 | 1.43 | 0.29 | 5.49 |
| Length | 0 | 0 | 55.89*** | 6.79 | 11.08 | 32.87** | 0.41 | 61.26** |
| Length2 | - | 0.23 | 0.06 | 28.42** | 2.49 | - | 0.14 | - |
| T X L | - | - | 21.77* | - | - | - | - | - |
| Error | 0 | 29.8 | 245.58 | 1255.70 | 184.73 | 167.96 | 14.99 | 217.12 |

were captured by large fish (Figure 4, Table 1). The behavior of silversides towards either of these zoeae generally did not change as exposure time increased, although the number of C. sapidus zoeae eaten decreased with time.

Zoeal behavior generally did not change during the course of the observation period (Figure 4, 5; Table 1). In the presence of large silversides or killifish, zoeal the behavior either did not change significantly, or the frequency of escape attempts decreased.

## DISCUSSION

Decapod zoeae which develop entirely within estuaries appear to have evolved better antipredatory adaptations than have those which are exported to coastal waters, where the risk of fish predation is predictably less. Feeding trials and behavioral observations both demonstrated that small silversides preferred small zoeae that are exported from the estuary (C. sapidus and U. minax) to large zoeae that are retained within estuaries (R. harrisii, S. reticulatum, and P. pugio). Behavioral observations also revealed that zoeae that complete their development in the lower estuary (P. ostreum) have better defenses against fish predation than the two species of larvae which develop in coastal waters.

Mud crab zoeae flared their spines following attacks and sometimes flexed their abdomens up over their carapace follwoing atacks. Other crab zoeae bearing spines also

can flare their antennal spines, but the spines were too short to observe them do so during the course of the ten-minute observation periods. However, mud crab zoeae, unlike other zoeae observed, possess a pair of abdominal spines that become erect when the abdomen is reflexed, further increasing their unpalatability. Zoeae did not evade attacks, but occasionally attempted to escape following attacks. Escape attempts were largely unsuccessful. Thus, zoeae primarily rely on their armor for protection.

Grass shrimp zoeae possess only a short rostral spine to deter attacks, but are much more effective than crab zoeae at escaping from fish. Shrimp zoeae, like crab zoeae, do not evade attack but rely on their spines and armor to survive initial attacks. Once released, shrimp zoeae can either swim very quickly in unpredictable loops or flex their abdomen to quickly traverse short distances. Because shrimp zoeae were initially difficult to handle, and because they can be difficult to recapture repeatedly, fish often appeared to lose interest. The combination of the very large body, short rostral spine and flexion response of P. pugio zoeae are as effective at preventing predation by small fishes as are the multiple spines of R. harrisii zoeae.

Zooplankters frequently have been described as either being evasive or armored. Copepods and some rotifers have light flexible exoskeletons or lorica and rely entirely on evasion for survival (Kerfoot, 1978; Gilbert and William-

son, 1979; O'Brien, 1979; Vinyard, 1980). Armored rotifers and cladocerans rely on postcontact defenses (e.g., spines, impenetrable and rigid protective carapaces and lorica, and passive sinking) for survival (Gilbert and Williamson, 1979; Gilbert and Stemberger, 1979; Havel and Dodson, 1984). However, helmeted cladocerans have been reported to have increased evasive capabilities relative to nonhelmeted forms (O'Brien and Vinyard, 1978; Grant and Bayly, 1981; Barry and Bayly, 1985; Mort, 1986). Shrimp zoeae are intermediates between the dichotomy of evasion versus armor that has arisen in the literature. They rely on armor to survive initial encounters and escape to prevent further interactions.

Unlike most crab zoeae, P. ostreum do not bear spines and rely primarily on behavioral rather than morphological defenses to deter fish predation. Pea crab zoeae are small, darkly pigmented, and have a smooth, brittle carapace. Behavioral observations revealed that P. ostreum zoeae tuck their abdomen closely beneath their cephalothorax following an attack and then remain motionless. Silversides captured the zoea repeatedly during the ten-minute observation period but did not consume it more often than other retained species. Pea crab zoeae may be rejected by fish because they resemble suspended inorganic particles in appearance, behavior and texture. After 24 h fish consumed as many pea crab zoeae as the two exported species of zoeae. Thus, passive sinking is about as effective as the spines of

other crab zoeae or the flexion response of P. pugio during brief encounters, but not when fed for an entire day to starved fish.

Behavioral observations also revealed that the effectiveness of the antipredatory adaptations diminished for mud crab, marsh crab, fiddler crab and grass shrimp zoeae as fishes increased in length. Small fishes are generally less able to capture and handle prey than are large ones (Durbin, 1979; Hunter, 1980; Unger and Lewis, 1983). However, small silversides generally did not have any more difficulty capturing and ingesting pea crab zoeae than did large fish larvae. The lack of spines and small body size permitted even the smallest fish examined to prey on pea crab zoeae. Larger silverside larvae also did not become more proficient at handling blue crab zoeae. Observations were conducted only on two size classes of silversides, both of which were capable of feeding on all blue crab zoeae presented within 24 h, whereas other zoeae were fed to fish which could not consume all zoeae offered. Thus fish did not experience as much difficulty preying on blue crab zoeae as on other zoeae. Furthermore, the similarity in body size and spine length of blue and fiddler crab zoeae would have probably otherwise resulted in similar behavioral responses of the fish towards the zoeae.

Fishes quickly learned to avoid spined prey, which not only increases the effectiveness of spines as an antipredatory trait, but may also increase the rate of evolution of

the character. Noxious prey are attacked less often by predators which can learn to avoid them. Therefore prey should be damaged and killed less frequently by predators capable of learning, which would enhance selection for the antipredatory adaptation. Zooplankton are patchily distributed, which favors short-term learning by fish to avoid noxious prey (Dill, 1983; Bronmark et al., 1984). Longterm memory of noxious prey also has been exhibited by fish (Kerfoot et al., 1980), so that spines may continue to reduce the attack frequency upon zoeae even if they have not been encountered recently. Silversides did not learn to avoid pea crab and blue crab zoeae for the same reasons that both large and small fish could readily prey on the zoeae (discussed above).

Silversides 20 and 40 mm long continued to show the same preferences for zoeae during 15-minute feeding trials as did smaller silversides during 10-minute feeding trials. Thus, the relative effectiveness of the antipredatory adaptations of the four species of crab zoeae is similar for larval and juvenile fish.

The antipredatory adaptations of mud crab zoeae also were more effective at preventing predation by larval killifish than were those of fiddler crab zoeae. Killifish were better able to capture and ingest both species of zoeae than were silversides of the same length, indicating that the larvae of large-mouthed demersal fishes may be best able to handle large, armored prey. Larval killifish are large

upon hatching and were able to prey on fiddler crab zoeae immediately. Larval killifish occur in large numbers in salt marshes where fiddler crabs release their larvae and could have a considerable impact on their hatching rhythms. Zoeae which are not effectively dispersed from tidal creeks would become subject to predation by killifish and shrimp which together number over 5000/m2 in tidal pools at low tide (Kneib, 1984). Thus, fiddler crab zoeae as well as other semiterrestrial crabs may hatch on nocturnal spring tides when the tidal volume in the upper estuary is the greatest to reduce stranding in tidal creeks (Christy, 1982).

## CONCLUSIONS

Larval killifish, larval silversides and juvenile silversides all preyed more readily on zoeae which are exported from the estuary than those which are retained within the estuary throughout their larval development. It is highly likely that those larvae which remain in estuaries have evolved morphologies and behavioral responses which enable them to withstand the intense predation pressure applied by the great abundance of fishes inhabiting estuaries. Zoeae which are vulnerable to fish predation morphologically have evolved behaviorally to undergo extensive horizontal migrations from the estuary into coastal waters where the risk of fish predation is reduced. Small estuarine crabs may be restricted to retaining their zoeae in estuaries simply because they cannot produce enough zoeae to

make exporting their zoeae a profitable alternative. Crabs producing few young have a greater investment in each offspring, and therefore zoeae are generally larger and better protected against predation. The large size of many retained zoeae may make them more obvious to fishes, but large size in combination with an armored exoskeleton and spines also makes them less palatable and more capable of surviving repeated attacks. Furthermore, fish quickly learn to avoid noxious prey and appear to be able to distinguish them from palatable prey which enhances the effectiveness of their antipredatory adaptations.

# LITERATURE CITED

Barry, M. J. and I. A. E. Bayly. 1985. Further studies on predator induction of crests in Australian Daphnia and the effects of crests on predation. Aust. J. Mar. Freshw. Res. 36: 519-535.

Bayliff, W. H., Jr. 1950. The life history of the silverside Menidia menidia (Linnaeus). Md. Bd. Nat. Res. 90: 1-25.

Bengston, D. A. 1984. Resource partitioning by Menidia menidia and Menidia beryllina (Osteichtheyes: Atherinidae). Mar. Ecol. Prog. Ser. 18: 21-30.

Bronmark, C., B. Malmqvist and C. Otto. 1984. Anti-predator adaptations in a neustonic insect. Oecologia 61: 189-191.

Cain, R. L. and J. M. Dean. 1976. Annual occurrence, abundance and diversity of fish in a South Carolina intertidal creek. Mar. Biol. 36: 369-379.

Christy, J. H. 1982. Adaptive significance of semilunar cycles of larval release in fiddler crabs (Genus Uca): test of an hypothesis. Biol. Bull. 163: 251-263.

Crabtree, R. E. and J. M. Dean. 1982. The sturcture of two South Carolina estuarine tide pool fish assemblages. Estuaries 5: 2-9.

Cronin, T. W. 1982. Estuarine retention of larvae of the crab Rhithropanopeus harrisii. Estuar. Coast. Shelf Sci. 15: 207-220.

Dill, L. M. 1983. Adaptive flexibility in the foraging behavior of fishes. Can. J. Fish. Aquat. Sci. 40:

398-408.

Derickson, W. K. and K. S. Price, Jr. 1973. The fishes of the shore zone of Rehoboth and Indian River bays, Delaware. Trans. Amer. Fish. Soc. 102: 552-562.

Dodson, S. I. 1984. Predation of Heterocope septentrionalis on two species of Daphnia: morphological defenses and their cost. Ecology 65: 1249-1257.

Durbin, A. G. 1979. Food selection by plankton feeding fishes. In: Clepper, M. (ed.), International Symposium on Predator-Prey Systems in Fish Communities and Their Role in Fisheries Management. Atlanta, Georgia, July 24-27, 1978. Sport Fishing Institute, Washington, D. C., 4: 203-218.

Flower, F. B. and J. J. McDermott. 1952. Observations on the occurrence of the oyster crab, Pinnotheres ostreum, as related to oyster damage in Delaware Bay. Proc. Nat. Shellfish. Assoc. Convention (1952), pp. 44-46.

Gilbert, J. J. and R. S. Stemberger. 1984. Asplanchna-induced polymorphism in the rotifer Keratella slacki. Limnol. Oceanogr. 29: 1309-1316.

Gilbert, J. J. and C. E. Williamson. 1979. Predator-prey behavior and its effect on rotifer survival in associations of Mesocyclops edax, Asplanchna girodi, Polyarthra vulgaris, and Keratella cochlearis. Oecologia 37: 13-22.

Gliwicz, Z. M. 1986. A lunar cycle in zooplankton. Ecology 67: 883-898.

Goy, J. W. 1976. Seasonal distribution and retention of some decapod crustacean larvae within the Chesapeake Bay, Virginia. MS Thesis, Old dominion University, Norfolk, VA. 334 pp.

Grant, J. W. G. and I. A. E. Bayly. 1981. Predator induction of crests in morphs of the Daphnia carinata King complex. Limnol. Oceanogr. 26: 201-218.

Havel, J. E. and S. I. Dodson. 1984. Chaoborus predation on typical and spined morphs of Daphnia pulex: behavioral observations. Limnol. Oceanogr. 29: 487-494.

Hunter, J. R. 1980. The feeding behavior and ecology of marine fish larvae. In: J. E. Bardach (ed.) The Physiological and Behavioral Manipulation of Food Fish as Production and Management Tools, pp. 287-330.

Kerfoot, W. C. 1978. Combat between predatory copepods and their prey: Cyclops, Epischura, and Bosmina. Limnol. Oceanogr. 23: 1089-1102.

Kerfoot, W. C., D. L. Kellogg, Jr. and J. R. Strickler. 1980. Visual observations of live zooplankters: evasion, escape, and chemical defenses. In: Evolution and Ecology of Zooplankton Communities. Kerfoot, W. C. (ed.), University Press of New England, Hanover, pp. 10-27.

Kneib, R. T. 1984. Patterns of invertebrate distribution and abundance in the intertidal salt marsh: causes and questions. Estuaries 7: 392-412.

Kneib, R. T. and A. E. Stiven. 1978. Growth, reproduction,

and feeding of Fundulus heteroclitus (L.) on a North Carolina salt marsh. J. Exp. Mar. Biol. Ecol. 31: 121-140.

McErlean, A. J., S. G. O'Conner, J. A. MLihursky and C. I. Gibson. 1972. Abundance, diversity and seasonal patterns of estuarine fish populations. Estuar. Coastal Mar. Sci. 1: 19-36.

Middaugh, D. P. 1981. Reproductive ecology and spawning periodicity of the Atlantic silverside, Menidia menidia (Pisces: Atherinidae). Copeia 1981: 766-776.

Millikin, M. R. and A. B. Williams. 1984. Synopsis of biological data on the blue crab, Callinectes sapidus Rathbun. NOAA Tech. Rep. NMFS 1: 1-39.

Morgan, S. G. 1987. Selection for spination of estuarine crab zoeae versus freshwater zooplankton. Ecol. Monogr.

Mort, M. A. 1986. Chaoborus predation and the function of phenotypic variation in Daphnia. Hydrobiologia 133: 39-44.

O'Brien, W. J. 1979. The predator-prey interaction of planktivorous fish and zooplankton. Amer. Sci. 67: 572-581.

O'Brien, W. J. and G. L. Vinyard. 1978. Polymorphism and predation: the effect of invertebrate predation on the distribution of two varieties of Daphnia carinata in South India ponds. Limnol. Oceanogr. 23: 452-460.

Pinschmidt, W. C. 1963. Distribution of crab larvae in relation to some environmental conditions in the

Newport River estuary, North Carolina. Ph.D. dissertation, Department of Zoology, Duke University, Durham, N. C., 112 pp.

Provenzano, A. J., Jr., J. R. McConaugha, K. B. Phillips, D. J. Johnson and J. Clark. 1983. Vertical distribution of first stage larvae of the blue crab, Callinectes sapidus, at the mouth of Chesapeake Bay. Estuar. Coast. Shelf Sci. 16: 489-499.

Richards, C. E. and M. Castagna. 1970. Marine fishes of Virginia's eastern (shore inlet and marsh, seaside waters). Chesapeake Sci. 11: 235-248.

Sandifer, P. A. 1973. Distribution and abundance of decapod crustacean larvae in the York River estuary and adjacent lower Chesapeake Bay, Virginia, 1968-1969. Chesapeake Sci. 14: 235-257.

Smith, S. M., J. G. Hoff, S. P. O'Neil and M. P. Weinstein. 1984. Community and trophic organization of nekton utilizing shallow marsh habitats, York River, Virginia. Fish. Bull. 82: 455-467.

Smyth, P. O. 1980. Callinectes (Decapoda: Portunidae) larvae in the middle Atlantic Bight, 1975-77. Fish. Bull., U.S. 78: 251-265.

Stitch, H. B. and W. Lampert. 1981. Predator evasion as an explanation of dirnal vertical migration by zooplankton. Nature (London) 293: 396-398.

Subrahmanyam, C. B. and S. H. Drake. 1975. Studies on the animal communities in two north Florida salt marshes.

Bull. Mar. Sci. 25: 445-465.

Targett, T. E. and J. D. McCleave. 1974. Summmer abundance of fishes in a Maine tidal cove with special reference to temperature. Trans. Amer. Fish. Soc. 1974: 325-330.

Thayer, G. W., D. E. Hoss, M. A. Kjelson, W. F. Hettler, Jr., and M. W. Lacroix. 1974. Biomass of zooplankton in the Newport River estuary and the influence of post--larval fishes. Chesapeake Sci. 15: 9-16.

Truesdale, F. M. and B. L. Andryszak. 1983. Occurrence and distribution of reptant decapod crustacean larvae in neritic Louisiana waters: July 1976. Contr. Mar. Sci. 26: 37-53.

Vinyard, G. L. 1980. Differential prey vulnerability and predator selectivity: effects of evasive prey on bluegill (Lepomis macrochirus) and pumpkinseed (L. gibbosus) predation. Can. J. Fish. Aquat. Sci. 37: 2294-2299.

Weinstein, M. P. 1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. Fish. Bull. 77: 339-356.

Zaret, T. M. and J. S. Suffern. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. Limnol. Oceanogr. 21: 804-813.

# CHAPTER 4

# THE IMPACT OF PLANKTIVOROUS FISHES ON THE LIFE HISTORIES OF ESTUARINE CRABS

## ABSTRACT

The effect of planktivory on the life history patterns of estuarine crabs was studied by determining the preferences of common estuarine fishes for crab zoeae in the laboratory and for populations occurring in the upper Newport River estuary, North Carolina. *Menidia menidia* and *Fundulus heteroclitus* 20, 40, 60 and 80 mm long preferred *Artemia* nauplii to crab zoeae in laboratory feeding trials, and both fishes, except 80 mm *M. menidia*, preferred *Uca minax* to *R. harrisii* zoeae. Plankton samples (68) and the three predominant species of fishes in the upper estuary were collected from an upstream and downstream location, on spring and neap low tides, and nocturnally and diurnally. Gut contents of 1911 *M. menidia*, *F. heteroclitus* and *Anchoa mitchelli* 15-100 mm long were analyzed. Over 99.6% of the plankters collected were decapod zoeae, copepods or barnacle larvae. Significantly higher densities of most zooplankters occurred upstream than downstream and on neap rather than spring tides. Thus, fishes generally preyed upon zooplankton most abundantly on neap tides at the upstream site. Crab zoeae that were most preferred by fishes, *Uca* and *Sesarma cinereum*, hatched on spring tides and were transported downstream, which may reduce the risk of fish predation. Decapod zoeae that were retained in the upper estuary, *Rhithropanopeus harrisii*, *S. reticulatum* and *Palaemonetes* were least preferred by fishes. Zoeae retained in the upper estuary have a greater total size (spine

length and body size), making them less vulnerable to fish predation than zoeae with short spines and small bodies, which are transported downstream. Fishes did not feed nocturnally when crabs hatch, which permits initial downstream dispersal of zoeae prior to sunrise. Zoeae did not diurnally vertically migrate in the upper estuary suggesting a reliance on armor during tidal vertical migrations required for the regulation of their position in the estuary. By allocating more resources per egg, crabs with abbreviated development (e.g., S. reticulatum vs. S. cinereum) produce large, well-armed zoeae with short planktonic durations, which permits the retention of zoeae in the upper estuary where the risk of fish predation is great. Small estuarine crabs are probably constrained to retain zoeae within the estuary because they cannot produce enough small zoeae to survive long migrations offshore to reduce the probability of encountering fishes. This study suggests that predation pressure exerted by planktivorous fishes is predictable in time and space, and the reproduction, hatching rhythms, dispersal patterns, and larval morphologies of estuarine crabs have evolved together to reduce the risk of planktivory regardless of the life history pattern exhibited.

## INTRODUCTION

Peak abundance of fishes in east coast estuaries occurs during the summer (Pearson, 1941; Warfel and Merriman, 1944; Wheatland, 1956; Richards, 1959; Springer and McErlean, 1962; Herman, 1963; Oviatt and Nixon, 1973; Hoff and Ibara, 1976; Orth and Heck, 1980; Judy, 1982; Kneib, 1984a; Rozas and Hackney, 1984; Hillman et al., 1977; Talbot and Able, 1984) in shallow, low salinity marshes and tidal pools and creeks of the upper estuary (Springer and Woodburn, 1960; Pearcy and Richards, 1962; Dovel, 1967; Cain and Dean, 1976; McErlean et al., 1972; Subrahmanyam and Drake, 1975; Hyle, 1976; Weinstein, 1979). The biomass of fishes in tidal pools of upper estuaries during summer has been determined to be 54.5-152.4 $g/m^2$ (Nixon and Oviatt, 1973; Crabtree and Dean, 1982), but only 1.84-6.33 $g/m^2$ in deeper portions of the estuaries (Turner and Johnson, 1973; Oviatt and Nixon, 1973), and 0.28-3.10 $g/m^2$ in the South Atlantic Bight (Wenner et al., 1979; Sedberry and Van Dolah, 1984). The great productivity and spatial complexity of salt marshes provide food and refuge for the large fish populations occurring there (Ryther, 1959; Malone, 1977; Ferguson et al., 1980; Boesch and Turner, 1984). Indeed, productivity estimates for marsh populations of killifish are among the highest reported for fish (Valiela et al., 1977; Meredith and Lotrich, 1979).

Larval fishes predominate in the upper estuary in summer (Subrahmanyam and Drake, 1975; Weinstein, 1979;

Crabtree and Dean, 1982; Rozas and Hackney, 1984; Talbot and Able, 1984), and are exclusively planktivorous (Hunter, 1980; Turner 1984). The great abundance of young fishes can have a considerable impact on estuarine zooplankton communities (Thayer et al, 1974; Bengston, 1984; Fulton, 1985). Many invertebrates also hatch during summer in temperate estuaries and their larvae may be under particularly intense predation pressure by the great abundance of planktivorous fishes.

Predators can determine the morphology and spatial and temporal distribution of their prey (Grant and Bayly, 1981; Blouw and Hagen, 1984; Gliwcz, 1986), and therefore the larval morphology and dispersal patterns of crabs also may have evolved in response to the predictable onshore-offshore gradient in fish predation. Zoeae that are retained within the estuary throughout development possess postcontact antipredatory adaptations which render them less susceptible to predation by small fishes compared to zoeae that make extensive migrations to coastal waters and reinvade the estuary as a megalopa (Morgan, 1987a). Retained zoeae bear longer spines and are larger than exported zoeae or they have evolved better evasive capabilities.

The timing of larval release also may be triggered by environmental cues to reduce predation (Johannes, 1978; Frank and Leggett, 1983). Estuarine crabs with zoeae that are especially vulnerable to predation hatch primarily on nocturnal spring high tides (Christy, 1982; Salmon et al.,

1986; Morgan, 1987b), so that zoeae are quickly flushed downstream into nearshore coastal waters up (Sandifer, 1975; Christy and Stancyk, 1982; Truesdale and Andryszak, 1985). Nearly all crab zoeae hatch nocturnally, probably to reduce fish predation. The eyes of larval fishes lack rods, which are sensitive to low light levels, and therefore fish larvae only feed diurnally (Braum, 1967; Blaxter, 1968, 1975; June and Carlson, 1971; Kjelson et al., 1975; Durbin, 1979; Hunter, 1980; Kawamura and Hara, 1980; Paul, 1983; Townsend, 1983; Hinshaw, 1985). Adult fishes that select small prey individually also generally feed diurnally (Hobson and Chess, 1978; Zaret, 1980a). However, moonlight can provide sufficient illumination for planktivory by diurnal fishes (Bohl, 1980; Zaret, 1980a; Townsend and Risebrow, 1982; Gliwicz, 1986), and larvae hatched on full moons may be particularly vulnerable to fish predation. Demersal fishes may feed either diurnally or nocturnally (Grossman, 1980; Jacob et al., 1983; Magnan and FitzGerald, 1984; Hoekstra and Jansen, 1985), and could prey on swarms of zoeae being hatched from burrows at night. Synchronized hatching may swamp nocturnal predators (Johannes, 1978).

In this paper, I will determine if the larval morphologies, dispersal patterns and hatching rhythms may have evolved in response to fish predation. First, I will determine the effectiveness of zoeal spines at deterring predation by juvenile and adult fishes when alternative prey is provided in the laboratory. Zoeae that are exported from

the estuary should be preferred to those that are retained. The preferences of bottom-feeding and planktivorous fishes for zoeae will be compared.

Furthermore, I will determine the electivities of fishes for zoeae in the upper estuary and see if they correspond to the relative preferences for zoeae as determined in the laboratory. The electivities of fishes will be monitored during day and night, spring and neap tides, and upstream and downstream locations. If virtually all crabs hatch at night to reduce fish predation on zoeae, then more zoeae should be consumed during the day rather than at night. If crab zoeae are transported downstream to reduce fish predation, then predation on crab zoeae should be greater upstream than downstream. If crabs hatch on spring tides to hasten downstream transport, then electivities for zoeae may be greater during neap than spring tides. Furthermore, synchronized hatching on spring tides may have evolved to swamp fish predators or to dilute larvae in the greatest volume of water. If predator swamping is to be effective then electivities for zoeae should not greatly increase during spring tides. The relationship among planktivory, abbreviated development, hatching rhtyhms, horizontal and vertical migration, larval morphology, and adult size is discussed.

## METHODS AND MATERIALS

### Electivities in the Laboratory

Gravid *R. harrisii* were collected for laboratory

experiments by using traps constructed out of wire mesh which lure crabs to the oyster shells contained within. Gravid U. minax were collected by digging up their burrows immediately prior to spring tides. Atlantic silversides, Menidia menidia, and the striped killifish, Fundulus heteroclitus, were seined from marshes and tidal creeks, respectively. All organisms were collected from the Neuse and Newport River estuaries, North Carolina.

Gravid crabs were placed in 19 cm culture dishes with 25 o/oo filtered water. Crabs were maintained in incubators at 25oC under a 12 h light: 12 h dark photoperiod until the larvae hatched. Fishes 20, 40, 60, and 80 mm SL were placed singly in 10 l circular tanks, and allowed to adjust to laboratory conditions for several days prior to experimentation. Fishes were maintained on Artemia nauplii.

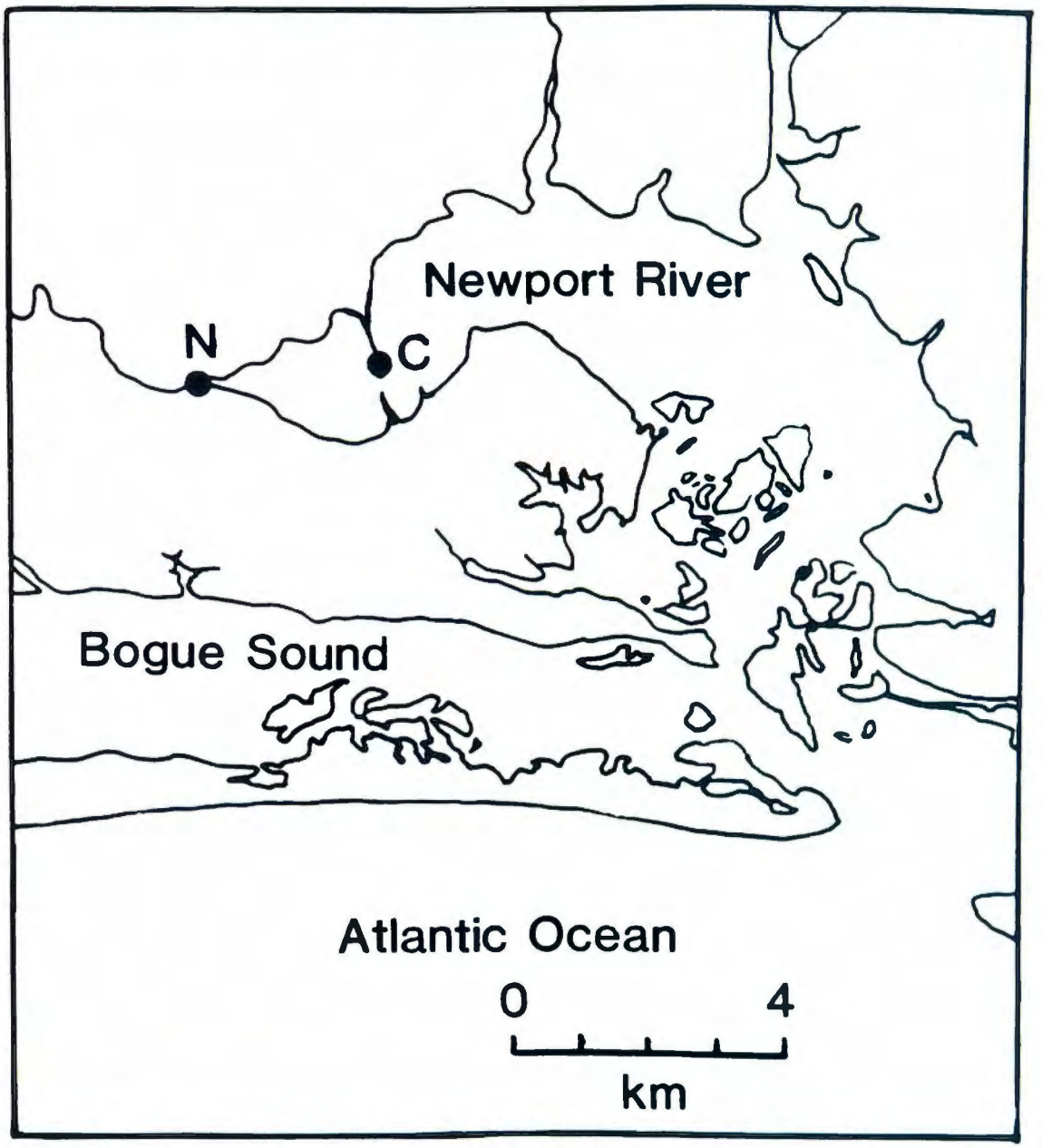
Three hundred crab zoeae of one species were fed to each fish along with enough Artemia nauplii to ensure that 10-40% of the nauplii remained after a 6-8 h period. This procedure enabled hungry fish to graze fairly indiscriminately initially, while still having enough prey remaining to reflect their subsequent preferences for prey. At the conclusion of the feeding trial all remaining prey were collected on a seive. The number of zoeae were counted before and after each feeding trial, and the number of Artemia nauplii were estimated by subsampling five aliquots of nauplii in a known volume of seawater. On the following day fish were fed 300 zoeae of the alternate species

together with the same quantity of Artemia nauplii. Ten replicates for each size class of fish species were conducted, except only two were performed for 20 mm silversides.

Electivities Determined in the Field

To determine electivities of fishes for zoeae in the field, fishes and plankton were collected in June and July from two sites in the Newport River estuary. The upstream site was located at the head of the estuary at the Newport Narrows (Figure 1). The second site was located at the Cross Rocks, a quarter of the way down the estuary, or 3.3 km downstream from the Newport Narrows. Samples were collected during the day on spring and neap low tides at both sites. Night samples also were collected at the downstream location on spring and neap low tides. A tidal creek just upstream from the Cross Rocks site also was sampled once on a nocturnal spring tide. Samples were collected at low tides because the largest numbers of fishes could be reliably seined then. Fishes were collected with a 16 m seine with 7 mm mesh. Plankton was collected using a plankton net with a 0.3 m diameter mouth and #10 mesh. All samples were preserved with formaldehyde. At least five plankton tows and three fish seinings were taken during each sampling period. The length of plankton tows was gauged using a flowmeter attached inside the mouth of the net, so that approximately 2 $m^3$ of water were sampled. A plastic seive (7 mm mesh) was attached inside the mouth of the collecting cup to exclude ctenophores. The presence of

Figure 1. Sampling sites (N=Newport Narrows, C=Cross Rocks) in the Newport River estuary, North Carolina.


Newport River
N
C
Bogue Sound
Atlantic Ocean
0
4
km

the ctenophore excluder probably also resulted in an underestimate of the number of other large zooplankters, such as fish, mysids and shrimp.

Plankton samples were split using a Folsom plankton splitter which is the most precise device for subsampling invertebrate plankters (Van Guelpen et al., 1982). One-eighth of the sample was counted under a dissecting microscope. Decapod zoeae were identified to species and instar, and other organisms were classified into broad taxa, e.g. copepods.

Gut contents were analyzed for the three most abundant species of fishes at the two sites: M. menidia, F. heteroclitus, and the bay anchovy, Anchoa mitchelli. Thirty specimens were analyzed, if available, for each of four size classes of fish: 15-25, 35-45, 55-65, and >65 mm. A total of 1933 stomachs were examined. After rinsing fishes in freshwater, stomachs were removed, slit longitudinally, and the contents washed into a grided watch glass. All prey items were enumerated. Decapod zoeae were identified to species and instar, and other taxa were lumped into broad categories as described above. Chesson's (1983) index of electivity was used to quantify the number of prey consumed relative to the number available for both gut content analyses of fishes collected from natural populations as well as for laboratory feeding trials. Electivities were determined for the nine most abundant plankters (exclusive

of hydromedusae which were not eaten), which accounted for 99.6% of all animals collected in the plankton net (Table 1). The remaining plankters were summed and grouped into an tenth category composed primarily of demersal and suspended benthic prey. Although demersal and benthic prey were under-represented in plankton samples, they were included in analyses because all prey items found in fish guts also were found in plankton samples. Furthermore, large fishes consumed many demersal prey and eliminating them from analyses appeared to bias electivities more than their inclusion. Gelantinous zooplankters were excluded from calculations of electivites because they were very rarely found in fish guts, and because ctenophores were excluded from entering the sample jar during plankton tows.

Gut retention time experiments were conducted for silversides maintained in 10 l containers at 28$^{o}$C and 25o/oo seawater. Twenty-four fish 40-60 mm long were fed 10,000 Artemia nauplii 24 h prior to the beginning of the experiment. During the experiment, fish were allowed to feed for one hour on field-caught plankton, which primarily contained copepods and Uca zoeae. Approximately 1000 copepods and Uca zoeae were fed to fish. Guts of three fish were examined immediately after the cessation of the one hour feeding period to ensure that fish were feeding and for comparison with subsequent samples. Seven fish each also were examined at 1, 3.5 and 5 hours following cessation of feeding.

Table 1. Mean (± SE) number of organisms per $m^3$ collected in plankton tows from the Newport River estuary, North Carolina.

| Taxon | Mean/m3 | SE |
|---|---|---|
| *Uca* zoeae | 8195.07 | 911.53 |
| Copepoda | 4541.22 | 392.66 |
| Barnacle Nauplii | 1168.05 | 146.66 |
| Hydromedusae | 401.74 | 87.21 |
| *S. reticulatum* zoeae I | 87.38 | 11.46 |
| Cyprids | 60.09 | 6.06 |
| *R. harrisii* zoeae I | 49.40 | 7.47 |
| *Palaemonetes* zoeae I-X | 37.21 | 3.00 |
| *S. cinereum* zoeae I | 14.64 | 3.19 |
| Gastropod veligers & juveniles | 12.77 | 3.22 |
| *R. harrisii* zoeae II | 9.21 | 2.14 |
| Ostracoda | 7.15 | 6.65 |
| Polychaete setigers | 6.99 | 1.12 |
| Fish Larvae | 6.03 | 1.30 |
| Mysidacea | 4.33 | 0.99 |
| *R. harrisii* zoeae III | 3.66 | 1.02 |
| Nematoda | 3.52 | 1.17 |
| Juvenile shrimp | 2.70 | 0.67 |
| *Mnemiopsis leidyii* | 2.62 | 0.82 |
| Foraminifera | 2.54 | 0.71 |

Table 1. (continued)

| | | |
|---|---|---|
| Amphipoda | 2.04 | 1.17 |
| *R. harrisii* zoeae IV | 1.81 | 0.53 |
| *Tomopterus* | 1.33 | 0.33 |
| Isopoda | 1.26 | 0.41 |
| Hymenoptera & Coleoptera | 1.23 | 0.39 |
| Chaetognatha | 1.08 | 0.27 |
| *S. reticulatum* zoeae II | 0.86 | 0.34 |
| *Pinnotheres ostreum* zoeae I | 0.73 | 0.27 |
| Brachyuran megalopae | 0.50 | 0.22 |
| Anomuran zoeae | 0.43 | 0.26 |
| *Pinnixa* zoeae | 0.40 | 0.16 |
| Cumacea | 0.28 | 0.14 |
| *P. herbstii* zoeae | 0.28 | 0.27 |
| *S. reticulatum* zoeae III | 0.20 | 0.18 |
| *Lucifer faxoni* | 0.05 | 0.05 |

## RESULTS

In laboratory feeding trials, all size classes of silversides and killifish avoided both species of crab zoeae in the presence of *Artemia* nauplii (Figure 2). Furthermore, all size classes of both fishes (except perhaps 80 mm silversides) preferred *U. minax* to *R. harrisii* (Figure 2, Table 2).

Mean numbers/$m^3$ of plankters collected are listed in Table 1. Higher densities of copepods, barnacle nauplii, cyprids, *Uca* spp., first instar *R. harrisii*, and first instar *S. reticulatum* occurred upstream than downstream, but more first instar *S. cinereum* and "others" were collected downsteam (Figure 3, Table 3). More copepods, barnacle nauplii, first instar *S. reticulatum* and *P. pugio* were collected on diurnal neap than spring tides, and there were no significant differences between tides for all other plankters. Of plankters collected only at the downstream site, barnacle nauplii and cyprids were most abundant during daylight hours, and copepods were most abundant at night. First instar *Uca* zoeae were most abundant on spring tides, and *S. cinereum* zoeae were most abundant on nocturnal spring tides.

*Menidia menidia*, *F. heteroclitus*, and *A. mitchelli* accounted for nearly all fish collected, but very small numbers of other species also were collected (Table 4). More species of fishes were collected downstream than

Figure 2. Mean electivity for *R. harrisii* and *U. minax* zoeae in the presence of *Artemia* nauplii by *M. menidia* and *F. heteroclitus* 20-80 mm long.

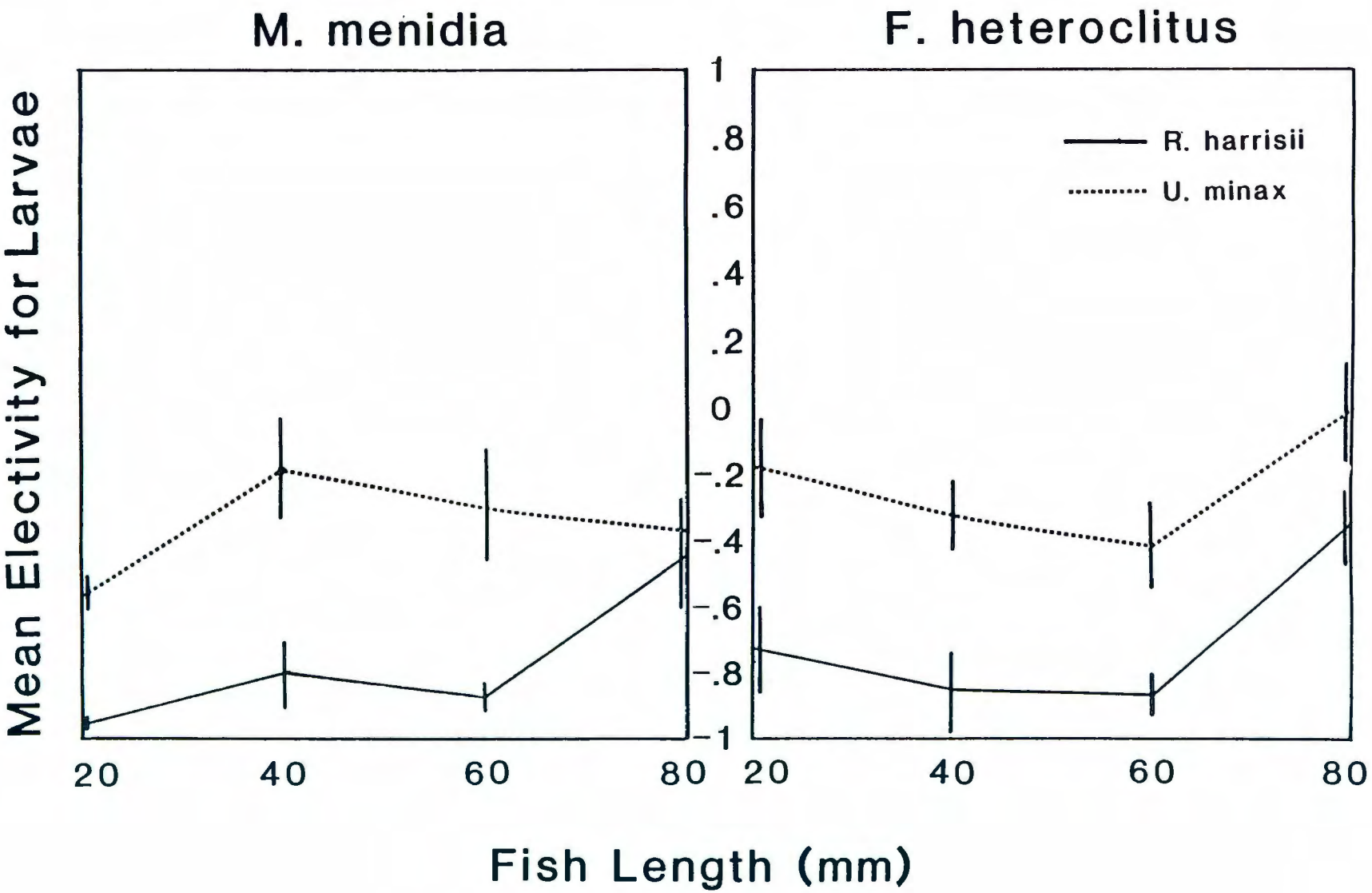

M. menidia
F. heteroclitus
Mean Electivity for Larvae
1
.8
.6
.4
.2
0
-.2
-.4
-.6
-.8
-1
R. harrisii
U. minax
20
40
60
80
20
40
60
80
Fish Length (mm)

Table 2. Analysis of variance of electivity of *M. menidia* and *F. heteroclitus* for *R. harrisii* and *U. minax* zoeae in the presence of *Artemia* nauplii (*=.05, **=.01, ***=.001 significance levels).

| Source | df | SS |
|---|---|---|
| *M. menidia* | 7 | 1.0683 |
| Zoeae | 1 | 0.4259*** |
| Fishlength | 3 | 0.1544* |
| Z X F | 3 | 0.2214** |
| Error | 56 | 0.8784 |
| | | |
| *F. heteroclitus* | 7 | 1.8007 |
| Zoeae | 1 | 1.0720*** |
| Fishlength | 3 | 0.6883*** |
| Z X F | 3 | 0.5344 |
| Error | 77 | 1.0974 |

Figure 3. Mean number of ten prey types collected/$m^3$ in the Newport River estuary by site, tide and time of day.

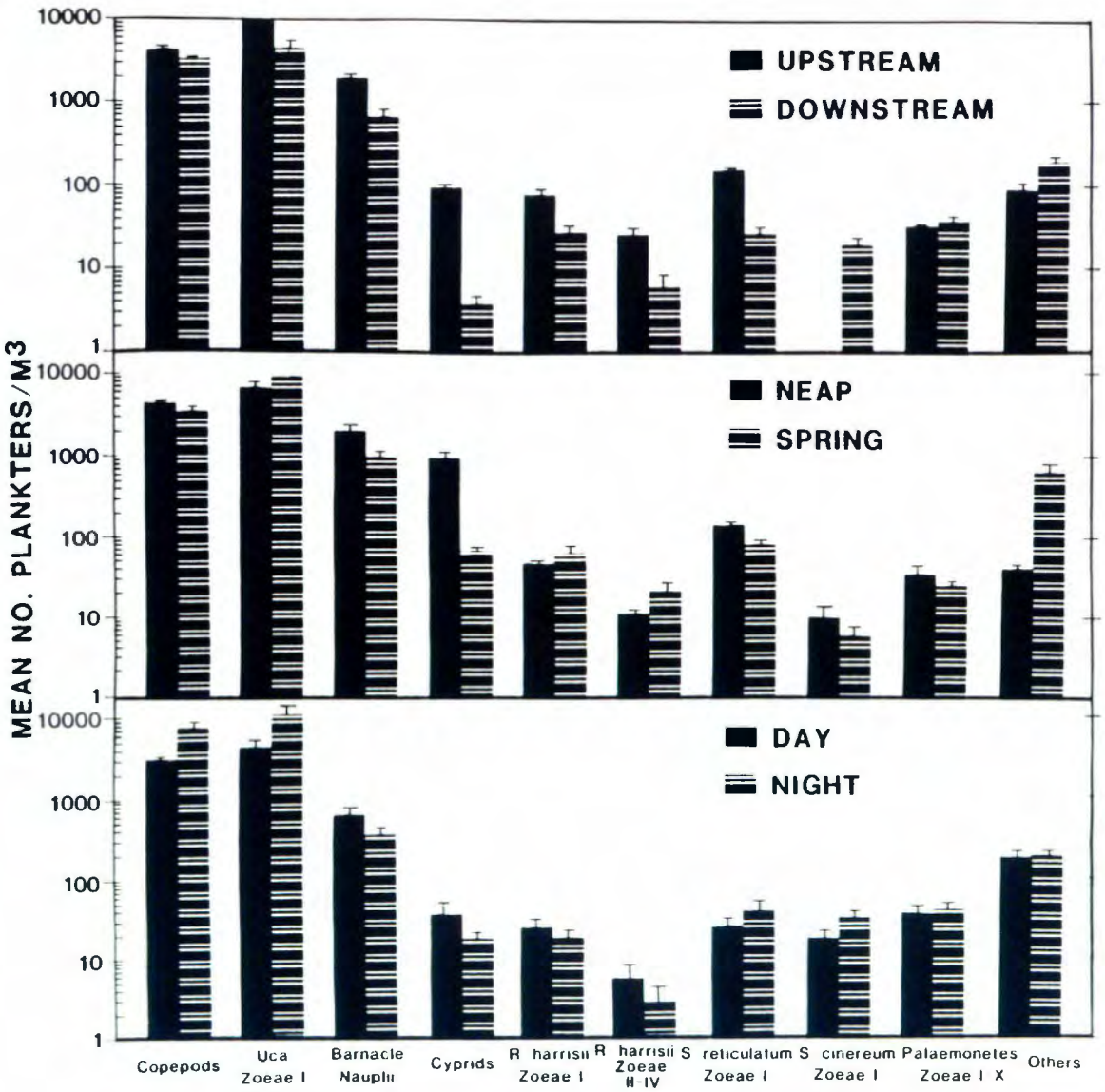

MEAN NO. PLANKTERS/M3
10000
1000
100
10
1
UPSTREAM
DOWNSTREAM
NEAP
SPRING
DAY
NIGHT
Copepods
Uca Zoeae I
Barnacle Naupli
Cyprids
R harrisii Zoeae I
R harrisii Zoeae II-IV
S reticulatum Zoeae I
S cinereum Zoeae I
Palaemonetes Zoeae I X
Others

Table 3. Analysis of variance of prey in the environment (species), of prey in fish guts, and electivities of fishes at upstream and downstream sites, on spring and neap tides, and during night and day for *M. menidia*, *A. mitchelli*, and *F. heteroclitus* collectively. Sums of squares and significance levels (*=.05, **=.01, ***=.001) reported.

| Source | Copepods | *Uca* Zoeae I | Barnacle | Cyprids | *R. harrisii* |
|---|---|---|---|---|---|
| Species | 32278056.26 | 395116237.16 | 39592350.65 | 42120.93 | 41015.14 |
| Site | 21179869.17* | 351177626.69*** | 26471681.03*** | 40119.13*** | 23817.75* |
| Tide | 15636116.45* | 8130534.24 | 17329200.83*** | 5213.76 | 293.22 |
| S X T | 3122.62 | 50147070.13 | 1438102.72 | 186.85 | 8730.21 |
| Error | 172641908.54 | 928805436.31 | 46134026.46 | 92104.25 | 193607.07 |
| Species | 462273077.10 | 1115422711.11 | 4448763.75 | 5021.00 | 4466.89 |
| Diel | 234305460.95*** | 226826678.77 | 605646.38** | 3352.19** | 66.39 |
| Tide | 233743154.54*** | 595379366.78** | 1246230.66*** | 30.78 | 4006.07** |
| D X T | 146546836.82*** | 265372032.21 | 1698965.89*** | 1784.85 | 0.97 |
| Error | 96395080.55 | 1927178176.00 | 2257476.35 | 17688.07 | 13669.84 |
| Guts | 578115.63 | 119009.27 | 2862.16 | 66.08 | 1.69 |
| Site | 112772.23*** | 114866.34*** | 2247.74*** | 57.09*** | 1.62*** |
| Tide | 207944.29*** | 1079.51 | 626.57*** | 18.72** | 0.03 |
| S X T | 183458.36*** | 1817.96 | 85.07 | 0.02 | 0.01 |
| Error | 9500535.18 | 5598080.18 | 65761.12 | 3002.64 | 183.35 |

Table 3. (continued)

| | | | | | |
|---|---|---|---|---|---|
| Guts | 686803.27 | 26489.09 | 868.36 | 13.28 | 0.0081 |
| Diel | 161812.06*** | 24361.86** | 201.72** | 1.70 | 0.0001 |
| Tide | 352579.24*** | 1235.65 | 203.19** | 7.67* | 0.0001 |
| D X T | 13283.89 | 1848.54 | 174.51* | 0.35 | 0.0073 |
| Error | 8446534.20 | 2822631.67 | 30410.21 | 1979.18 | 2.9836 |
| | | | | | |
| Electivity | 1.9531 | 2.6316 | 3.0207 | 2.5742 | 0.0399 |
| Site | 1.4096** | 0.4926** | 2.3321*** | 2.1902*** | 0.0390*** |
| Tide | 0.0442 | 0.4926*** | 0.0056 | 0.0442 | 0.0017 |
| S X T | 0.8832* | 1.4470*** | 0.1594* | 0.0188 | 0.0001 |
| Error | 191.8469 | 60.0067 | 34.9794 | 58.7635 | 2.8297 |

| Source | R. harrisii Zoeae II-IV | S. reticulatum Zoeae I | S. cinereum Zoeae I | Palaemonetes Zoeae I-X | Others |
|---|---|---|---|---|---|
| Species | 8026.29 | 316020.34 | 4347.48 | 7519.56 | 5553681.84 |
| Site | 2689.23 | 253575.67*** | 4140.45*** | 5.67 | 3424909.87* |
| Tide | 274.81 | 60415.37*** | 5.45 | 6964.44*** | 180635.74 |
| S X T | 3119.41 | 46832.96** | 5.45 | 1054.03 | 760138.84 |
| Error | 37702.38 | 209541.22 | 11204.10 | 16394.86 | 26263629.36 |
| | | | | | |
| Species | 920.99 | 8231.48 | 5921.99 | 6205.14 | 131397.74 |
| Diel | 29.30 | 783.29 | 896.64 | 29.02 | 890.34 |
| Tide | 710.46** | 2407.23 | 2363.14 | 1207.68 | 114843.34** |
| D X T | 29.30 | 5337.35* | 2748.43 | 3587.50* | 674.10 |
| Error | 1961.30 | 25687.81 | 21922.80 | 25544.07 | 288544.55 |
| Guts | 0.0236 | 12.32 | 19.91 | 546.10 | 1203.42 |

Table 3. (continued)

| | | | | | |
|---|---|---|---|---|---|
| Site | 0.0229* | 4.39 | 15.02*** | 157.15 | 292.32* |
| Tide | 0.0003 | 7.90 | 1.24 | 166.45 | 38.82 |
| S X T | 0.0003 | 0.89 | 1.24 | 151.66 | 942.82*** |
| Error | 7.9531 | 3928.96 | 1083.13 | 115193.59 | 78450.75 |
| | | | | | |
| Guts | 0 | 13.23 | 9.49 | 456.29 | 1361.20 |
| Diel | 0 | 5.15 | 6.20* | 94.69 | 564.24*** |
| Tide | 0 | 2.26 | 2.00 | 121.25 | 313.52** |
| D X T | 0 | 2.26 | 0.14 | 84.76 | 142.45 |
| Error | 0 | 2889.46 | 1109.21 | 115198.25 | 48906.60 |
| | | | | | |
| Electivity | 0.0029 | 0.1945 | 0.8887 | 0.1100 | 14.87 |
| Site | 0.0024* | 0.1706*** | 0.8070*** | 0.0219 | 14.09*** |
| Tide | 0.0007 | 0.0002 | 0.0001 | 0.0619* | 0.04 |
| S X T | 0.0007 | 0.0004 | 0.0001 | 0.0001 | 1.07** |
| Error | 0.4968 | 14.7653 | 22.9631 | 13.3934 | 205.17 |

upstream, but fishes appeared to be much more abundant upstream.

The food habits of M. menidia, F. heteroclitus and A. mitchelli are presented in Figure 4. More barnacle nauplii, cyprids and first instar Uca, R. harrisii, and S. reticulatum zoeae were consumed at the upstream site, and more copepods, first instar S. cinereum, and "others" were eaten at the downstream site (Figure 5, Table 3). Highest electivities for copepods, first instar Uca zoeae, barnacle nauplii, cyprids, R. harrisii, and first instar S. reticulatum zoeae occurred at the upstream site, but electivities downstream were highest for first instar S. cinereum and "others" (Figure 6, Table 3). More copepods, barnacle nauplii, and cyprids were consumed on neap than spring tides (Figure 5, Table 3). Fishes preferred first instar Uca zoeae when feeding on spring rather than neap tides, whereas greater electivities were obtained for fishes preying on Palaemonetes zoeae on neap tides (Figure 6, Table 3). At the downstream site, fishes did not prey on greater numbers of any plankter at night, but did eat more copepods, first instar Uca zoeae, barnacle nauplii, first instar S. cinereum zoeae, and "others" during daylight hours (Figure 5, Table 3).

The length of fishes differed between the two sites. The guts of 30 fishes were examined for each size class of fish for each sampling period if available. If fewer fish

Table 4. List of fishes collected at the Newport Narrows (upstream) and Cross Rocks (downstream) sites.

| Species | Newport Narrows | Cross Rocks |
|---|---|---|
| Menidia menidia | X | X |
| Anchoa mitchelli | X | X |
| Fundulus heteroclitus | X | X |
| Fundulus majalis | | X |
| Mugil cephalus | X | X |
| Leiostomus xanthurus | X | X |
| Micropogonius undulatus | X | X |
| Cynoscion spp. | X | X |
| Bairdiella chrysura | X | X |
| Lagodon rhomboides | X | X |
| Paralichthys spp. | X | X |
| Trinectes maculatus | X | X |
| Symphurus plagiusa | X | X |
| Strongylura marina | X | X |
| Pomatomus saltatrix | X | X |
| Opsanus tau | | X |
| Anguilla rostrata | | X |
| Syngnathus spp. | | X |
| Synodus foetens | | X |
| Selene vomer | | X |
| Caranx hippos | | X |

Table 4. (continued)

| | |
|---|---|
| *Monocanthus hispidus* | X |
| Gobiidae | X |

Figure 4. Percent occurrence of ten prey types in the guts of M. menidia (Mm), A. mitchelli (Am) and F. heteroclitus (Fh) 20-80 mm long. The number above each bar indicates the number of guts examined.

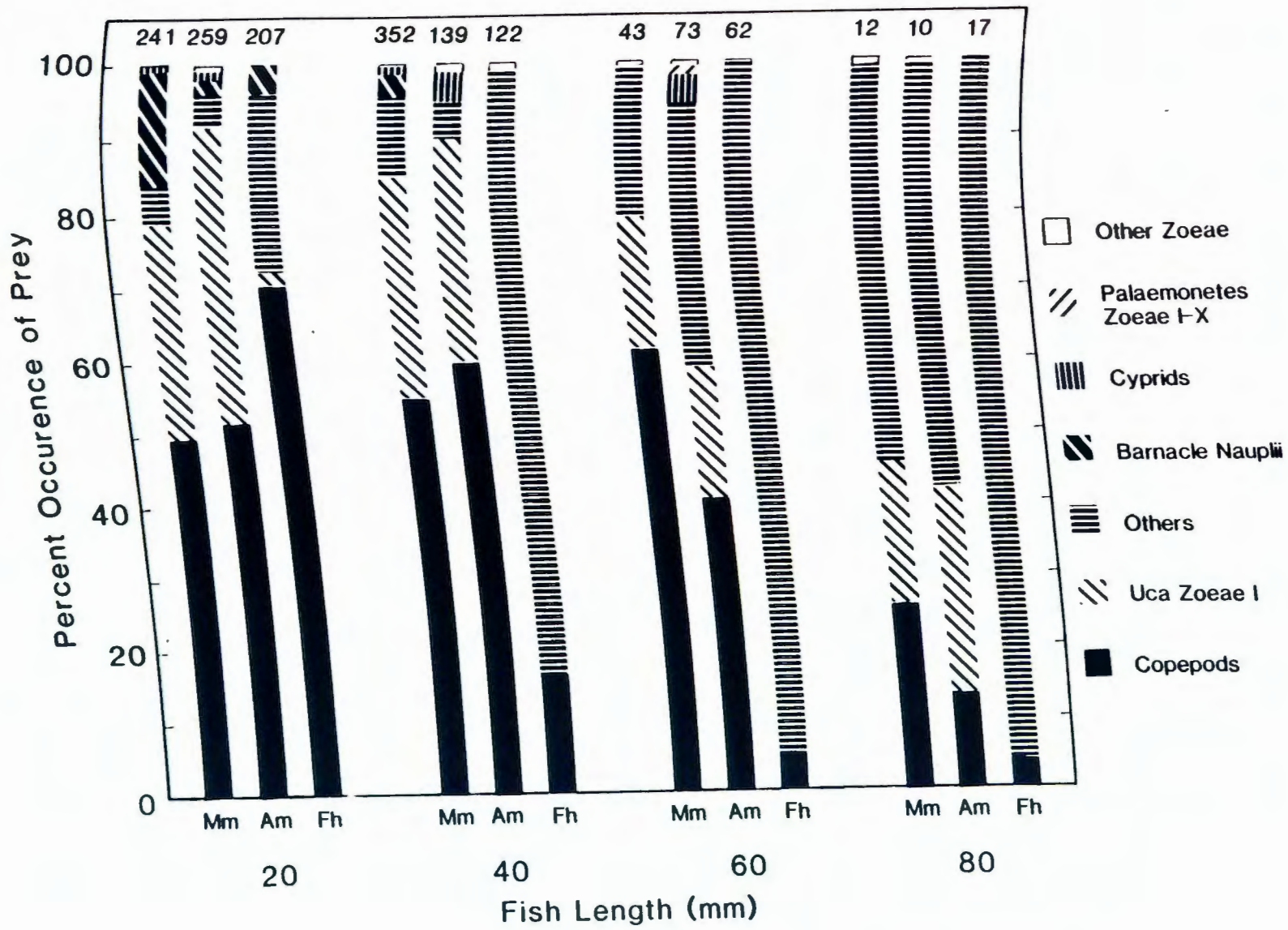

241 259 207
352 139 122
43 73 62
12 10 17
100
80
60
40
20
0
Percent Occurence of Prey
Mm Am Fh
Mm Am Fh
Mm Am Fh
Mm Am Fh
20
40
60
80
Fish Length (mm)
Other Zoeae
Palaemonetes Zoeae I-X
Cyprids
Barnacle Nauplii
Others
Uca Zoeae I
Copepods

Figure 5. Mean number of ten prey types in the guts of *M. menidia*, *F. heteroclitus* and *A. mitchelli* collected in the Newport River estuary by site, tide and time of day.

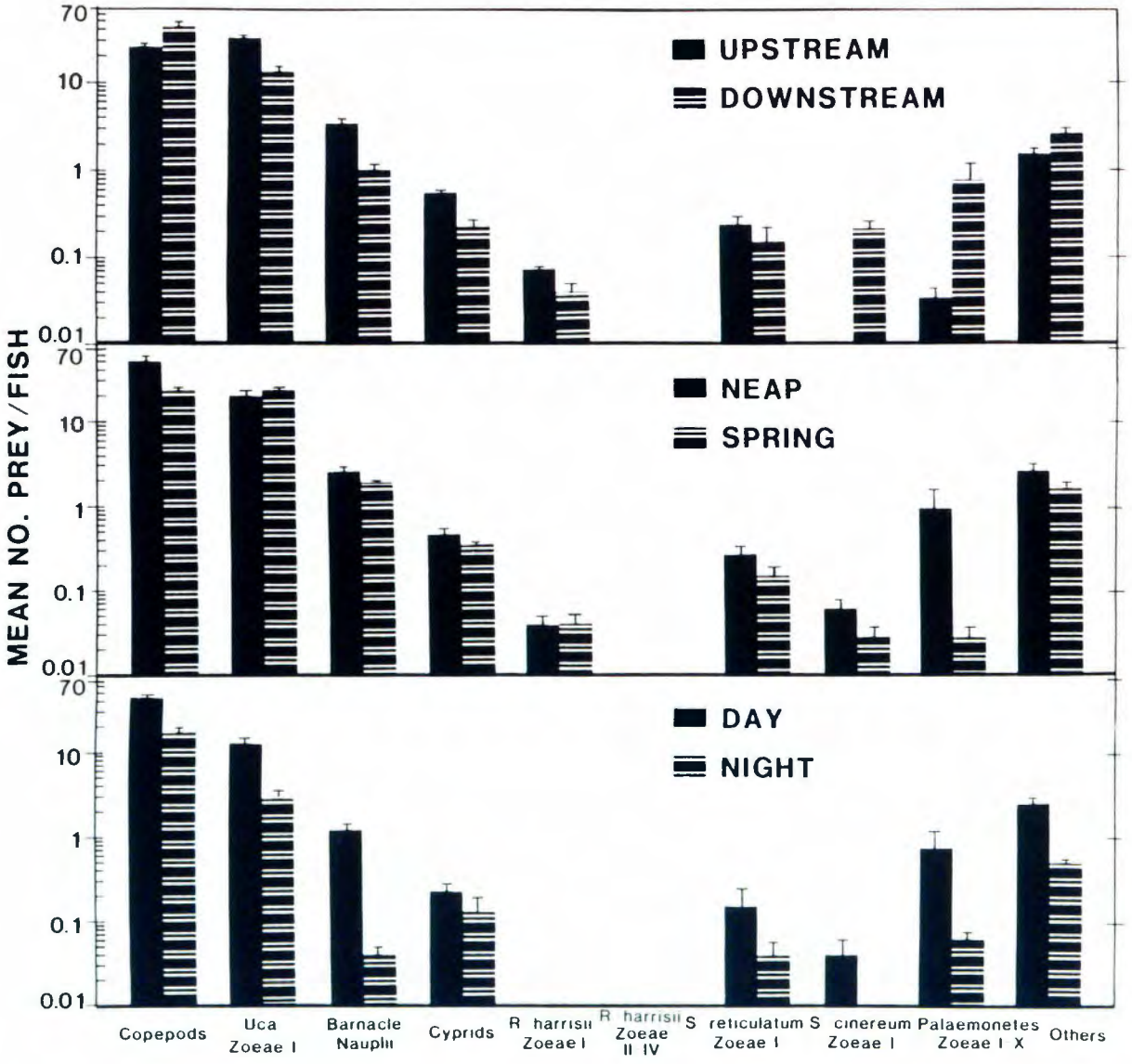
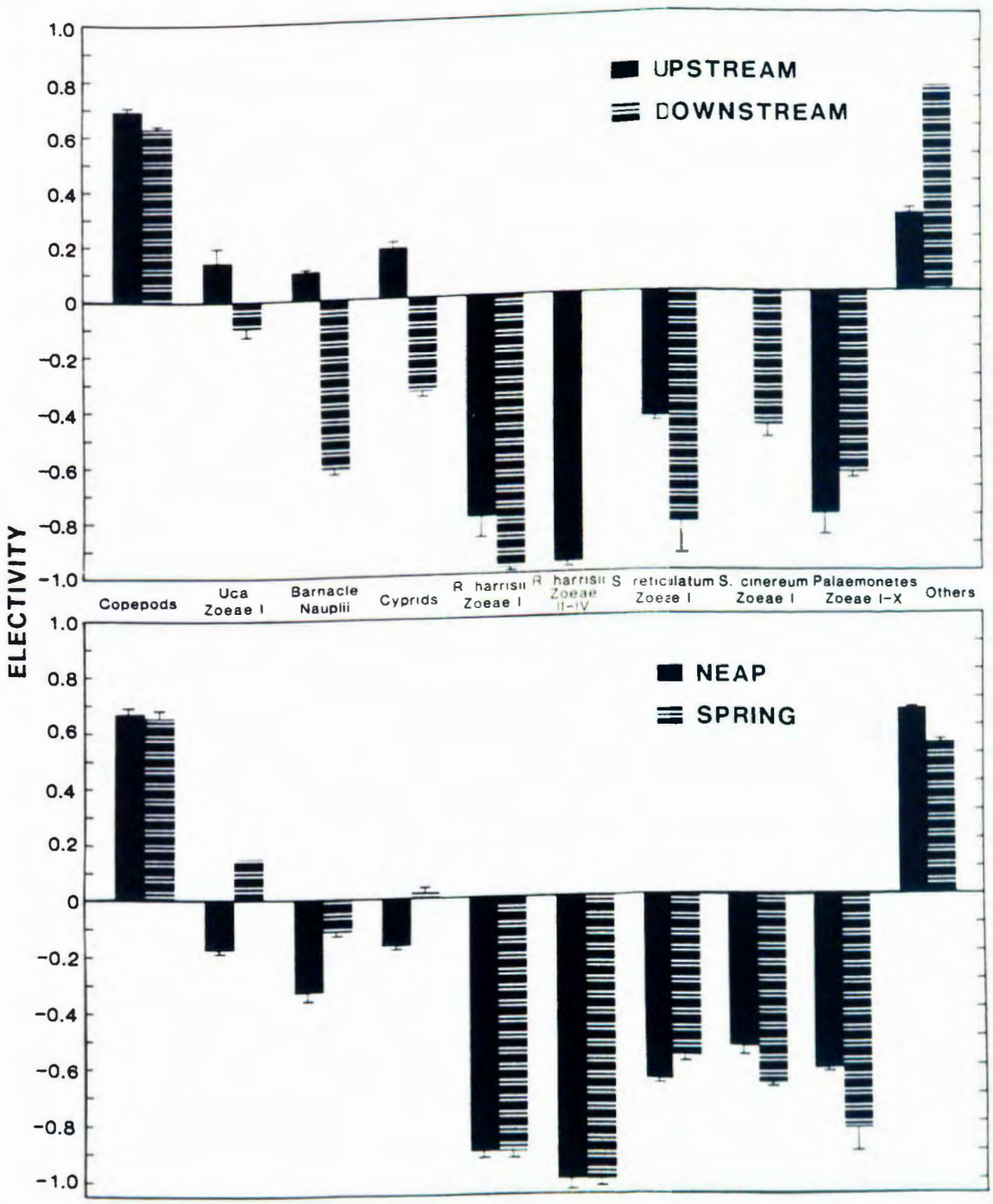

MEAN NO. PREY/FISH
70
10
1
0.1
0.01
UPSTREAM
DOWNSTREAM
NEAP
SPRING
DAY
NIGHT
Copepods
Uca Zoeae I
Barnacle Nauplii
Cyprids
R harrisii Zoeae I
R harrisii Zoeae II IV
S reticulatum Zoeae I
S cinereum Zoeae I
Palaemonetes Zoeae I X
Others

Figure 6. Mean electivity of *M. menidia*, *A. mitchelli* and *F. heteroclitus* for ten prey types collected in the Newport River estuary by site, tide and time of day.


ELECTIVITY
1.0
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1.0
UPSTREAM
DOWNSTREAM
Copepods
Uca Zoeae I
Barnacle Nauplii
Cyprids
R. harrisii Zoeae I
R. harrisii Zoeae II-IV
S. reticulatum Zoeae I
S. cinereum Zoeae I
Palaemonetes Zoeae I-X
Others
NEAP
SPRING

were analyzed for a size class it was because fewer than 30 were available. The numbers of 20, 40, 60 and 80 mm fishes analyzed at the upstream site were 435, 309, 23 and 4, and the numbers at the downstream site were 253, 309, 157, 43. Although the same numbers of 40 mm fishes occurred at both sites, more 20 mm fishes were collected upstream and more 60 and 80 mm fishes were found downstream.

Small fishes (less than 45 mm) preferred copepods, first instar Uca zoeae, barnacle nauplii, cyprids, and first instar S. reticulatum zoeae, and large fishes (greater than 55 mm) preferred "others" (Figure 4, Table 5). Small killifish preferred copepods, and barnacle nauplii, and large killifish preferred "others". Killifish did not consume R. harrisii, S. reticulatum, or S. cinereum zoeae. Small silversides preferred barnacle nauplii and cyprids, and large silversides preferred first instar S. cinereum, Palaemonetes, and "others". Small anchovies preferred copepods, first instar Uca zoeae, and barnacle nauplii, and large anchovies preferred first instar R. harrisii and "others". The preferences of all size classes combined for each fish species and for all fishes combined for the ten prey categories were ranked and are presented in Table 6.

Fishes also frequently consumed large amounts of detritus. Detritus was present in 85% of killifish guts and 32% of silverside guts at the upstream site, and 6% and 1%

Table 5. Analysis of variance of electivities of fishes less than 45 mm and greater than 55 mm. Total degrees of freedom: *M. menidia*= 662; *A. mitchelli*=477; *F. heteroclitus*=441; Total= 1584. Significance levels: *=.05, **.01, ***=.001.

| Source | *M. menidia* SS | *A. mitchelli* SS | *F. heteroclitus* SS | Total SS |
|---|---|---|---|---|
| Copepods | 0.00004 | 2.3781*** | 10.6820*** | 9.1982*** |
| Error | 93.96063 | 64.1418 | 63.7635 | 226.7460 |
| *Uca* Zoeae I | 0.0945 | 0.8643** | 0.0034 | 0.8251*** |
| Error | 25.0044 | 43.0821 | 1.3353 | 78.5511 |
| Barnacle Nauplii | 0.6090*** | 0.0484* | 0.0955* | 0.9534*** |
| Error | 25.6820 | 4.2884 | 6.5407 | 39.2262 |
| Cyprids | 0.9341*** | 0.1358 | 0.0071 | 1.1657*** |
| Error | 37.1745 | 32.6391 | 1.6633 | 75.8593 |
| *R. harrisii* I | 0.0051 | 0.0194** | 0 | 0.0002 |
| Error | 2.5438 | 1.2219 | 0 | 3.8237 |
| *R. harrisii* II-IV | 0.0017 | 0.00002 | 0 | 0.0002 |
| Error | 0.4597 | 0.03749 | 0 | 0.4997 |

Table 5. (continued)

| | | | | |
|---|---|---|---|---|
| *S. reticulatum* I | 0.0082 | 0.0563 | 0 | 0.0672** |
| Error | 7.6358 | 7.0902 | 0 | 15.0433 |
| *S. cinereum* I | 0.2267*** | 0.0270 | 0 | 0.0070 |
| Error | 12.5300 | 14.5178 | 0 | 27.7807 |
| *Palaemonetes* I | 0.1370** | 0.0010 | 0.0004 | 0.0102 |
| Error | 8.4712 | 7.4603 | 0.6766 | 16.9064 |
| Others | 1.7790*** | 13.5271*** | 13.3470*** | 37.1838*** |
| Error | 2.3242 | 28.8532 | 7.7104 | 40.3747 |

Table 6. Ranked electivities (E) of *M. menidia*, *A. mitchelli*, *F. heteroclitus* and overall for prey in the Newport River estuary, North Carolina.

| Prey | Total | | *M. menidia* | | *A. mitchelli* | | *F. heteroclitus* | |
|---|---|---|---|---|---|---|---|---|
| | E | Rank | E | Rank | E | Rank | E. | Rank |
| Copepods | .66 | 1 | .67 | 1 | .69 | 1 | .61 | 2 |
| Others | .59 | 2 | .29 | 2 | .36 | 3 | .88 | 1 |
| *Uca* zoeae I | .06 | 3 | .07 | 5 | .38 | 2 | -.90 | 5 |
| Cyprids | -.06 | 4 | .19 | 3 | .03 | 4 | -.86 | 4 |
| Barnacle Nauplii | -.24 | 5 | .08 | 4 | -.64 | 8 | -.56 | 3 |
| *S. cinereum* I | -.59 | 6 | -.55 | 6 | -.38 | 6 | - | - |
| *S. reticulatum* I | -.75 | 7 | -.53 | 7 | -.52 | 5 | - | - |
| *Palaemonetes* I-X | -.81 | 8 | -.62 | 8 | -.62 | 7 | -.96 | 6 |
| *R. harrisii* I | -.90 | 9 | -.82 | 9 | -.92 | 9 | - | - |
| *R. harrisii* II-IV | -.98 | 10 | -.97 | 10 | -.99 | 10 | - | - |

of killifish and silverside guts, respectively, at the downstream location. Only one of 501 anchovies examined from both sites contained detritus. The guts of most of these killifish were packed fully with detritus, and frequently contained very few prey. Silversides did not fill their guts with detritus as often as killifish, and more prey were usually present.

Examinations of the guts of silversides immediately after the cessation of feeding revealed the guts were entirely packed with undigested prey. After one hour, the guts of four fish were filled with zooplankton and three had stomachs which were slightly less full. After 3.5 h, three fish had remains in their stomachs and four fish only had identifiable prey in their mid- and hindguts. After five hours, all seven fish had empty stomachs and midguts.

## DISCUSSION

### Fish Predation on Zoeae

The upper estuary was dominated by silversides, killifish and anchovies, as is typical for other east coast estuaries (Warfel and Merrimen, 1944; Springer and Woodburn, 1960; Springer and McErlean, 1962; Herman, 1963; Croker, 1965; Dovel, 1967; Fiske et al., 1966; Mulkana, 1966; Briggs and O'Conner, 1971; Curley et al., 1971; McErlean, et al., 1972; Hillman et al., 1977; Targett and McCleave, 1974; Briggs, 1975; Subrahmanyam and Drake, 1975; Cain and Dean, 1976; Hoff and Ibara, 1976; Weinstein, 1979; Birely, 1984; Kneib, 1984a; Talbot and Abele, 1984). These fishes are

year round residents of the upper estuary and its tidal creeks (Derickson and Price, 1973; Richards and Castagna, 1970; Shenker and Dean, 1979; Crabtree and Dean, 1979), although silversides migrate from New England estuaries during winter (Conover and Ross, 1982). Thus, because these three fishes predominate year round throughout estuaries, it is likely that the reproductive and larval ecology of crabs, and particularly those that release zoeae into tidal creeks of the upper estuary, have evolved in response to their presence.

Silversides and anchovies would appear to have the greatest impact on the larval biology of crabs, because they feed on zoeae throughout their lives. Dietary surveys of fishes from other estuaries also indicate that anchovies frequently prey on crab zoeae (Springer and Woodburn, 1960; Carr and Adams, 1978; Spight, 1981; Smith et al., 1984), and to a lesser extent silversides do as well (Mulkana, 1966; Lucas, 1982). Anchovies were the main predator on zoeae which are retained in the estuary, due to their ability to handle large difficult prey.

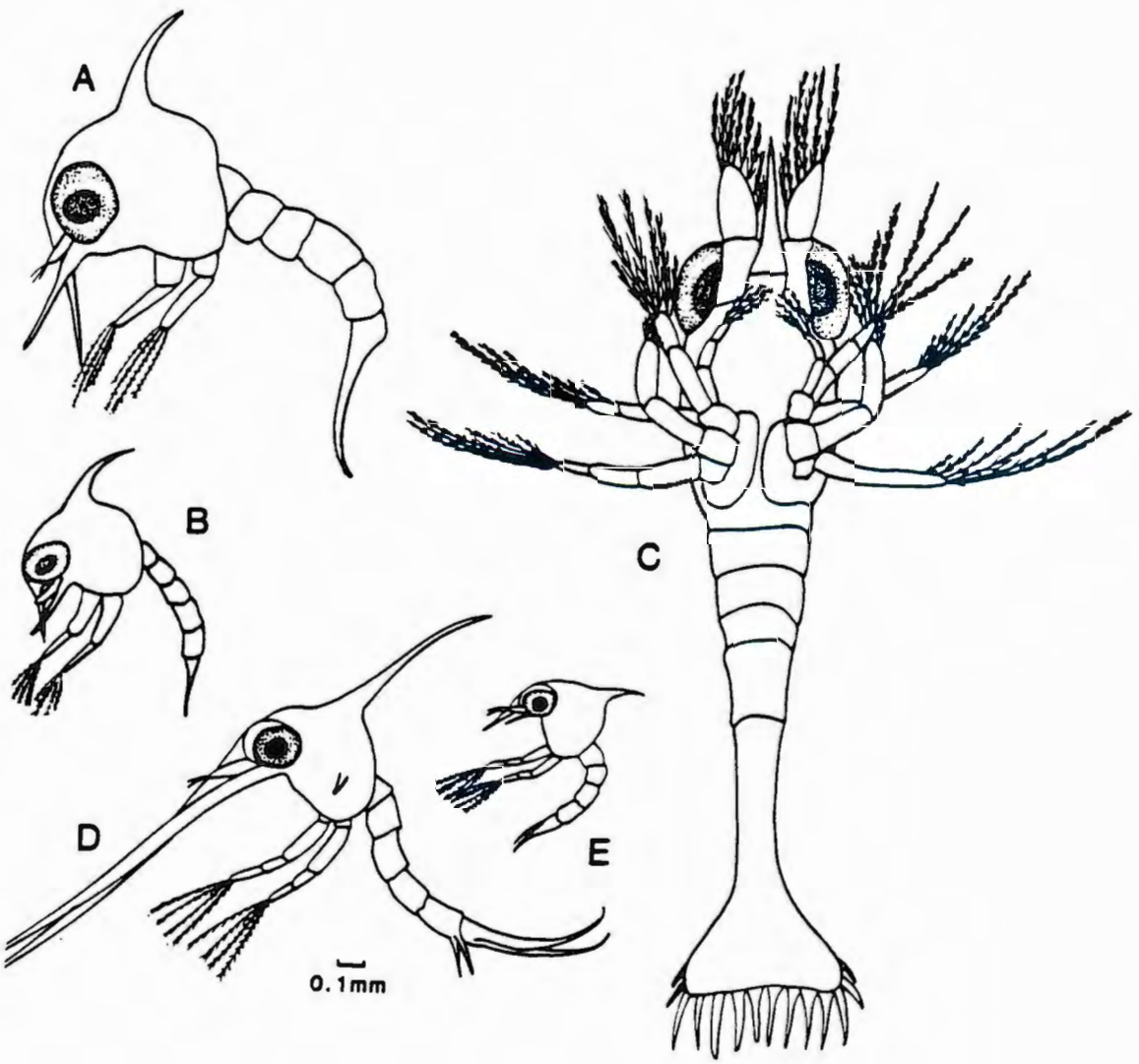
Killifish probably exert the least impact on populations of crab zoeae of the three fish species examined. Kneib (1986) found that killifish frequently consumed crab zoeae, but other surveys of the food habits of the killifish indicated that crab zoeae were not preyed upon (Kneib and Stiven, 1976; Penczak, 1985). In this study, killifish did not feed on R. harrisii, S. cinereum, or S. reticulatum

zoeae, although they preyed on other plankters (primarily calanoid copepods and small numbers of the most abundant zooplankter, Uca zoeae). Killifish feed on the marsh surface when it is inundated by tides, and in tidal creeks and pools at low tide (Kneib, 1984a). Crab zoeae probably disperse rapidly from marshes and tidal creeks, and therefore are not frequently encountered by killifish. Silversides and anchovies often forage in the river channel outside tidal creeks (Butner and Brattstrom, 1960; Crabtree and Dean, 1979).

Fish Predation and Zoeal Morphology

The electivities of silversides for crab zoeae and Artemia nauplii determined in the laboratory were relatively similar to those found for silversides collected from the field. Abundant alternative prey (Artemia nauplii in the laboratory or copepods in the field) were much preferred to crab zoeae. The noxious spines of zoeae (Morgan, 1987c) deter even adult fishes from preying on zoeae when spineless prey are available. Furthermore, Uca zoeae were preferred to R. harrisii zoeae by most size classes of silversides in the laboratory (all except 80 mm fish) as well as in the field. Rhithropanopeus harrisii zoeae are larger and bear longer spines than do Uca zoeae (Figure 7), so that silversides of all sizes experienced greater difficulty preying on the zoeae of R. harrisii than Uca. After R. harrisii, the next largest zoeae was S. reticulatum, followed by S. cinereum (Figure 7). Fishes in the field preferred the

Figure 7. First instar zoeae of A) *S. reticulatum*, B) *S. cinereum*, C) *P. pugio*, D) *R. harrisii*, and E) *U. minax*.


A
B
C
D
E
0.1mm

smallest species of crab zoeae, and their preferences for the remaining species declined as the total size (body plus spines) of zoeae increased. The negative effect of zoeal size is demonstrated more directly by the greater preference of fishes for small first instar R. harrisii zoeae than for large later instar R. harrisii zoeae.

The large difference in electivities of fishes for Uca and S. cinereum zoeae is partially due to the difference in their size, but also probably resulted from the rarity of the latter. Electivity is affected by the absolute abundance of prey and its relative abundance to other prey, so that when densities of a particular prey are low, predators consume disproportionately more of an abundant prey type (Werner and Hall, 1974; Murdoch et al., 1975; Bohl, 1982; Rajasilta and Vuorinen, 1983; Magnhagen, 1985). Furthermore, electivity values should be considered only as indications of the relative preferences for prey by a predator. Different electivity indices yield various absolute values, and it is difficult to obtain representative samples from the predator's habitat (Kohler and Ney, 1982; Lechowicz, 1982).

Evasion is less effective than spination at deterring fish predation. The shrimp zoea has a much larger body than R. harrisii zoeae, but is armed only with a short rostral spine (Figure 7). However, shrimp zoeae were preferred to R. harrisii zoeae despite the larger body size and superior evasive capabilities of P. pugio zoeae (Morgan, 1987a).

Thus, long multiple spines of zoeae appear to be most effective at deterring fish predation. Furthermore, even zoeae bearing short spines are less preferred than unarmored evasive prey. In freshwaters the evasive capabilities of copepods make them less preferable to fish than cladocerans of similar size (Vinyard, 1980). However in this survey, copepods were less abundant than Uca zoeae but still were preferred. Thus, fishes preferred evasive copepods to the short spines of the most vulnerable zoeae.

A great body of literature has documented that fish prefer the largest prey available, but it must be emphasized that preferences for the largest zooplankters occur only if they do not possess morphological or behavioral adaptations to deter fish predation. Crab zoeae with the greatest total size (body plus spines) are less susceptible to fish predation, and large copepods evade capture more frequently than do small ones (Vinyard, 1980; Bohl, 1982). Thus, morphological and behavioral antipredatory adaptations make large zooplankters more difficult to capture or handle than smaller prey.

Fish Predation and Larval Dispersal

The risk of predation is greatest upstream in shallow, narrow areas in the upper estuary. The cross sectional area of the Newport River estuary at the upstream site was much smaller than at the downstream site (Figure 1), which is concommitant with significantly higher densities of most zooplankters upstream. Zooplankton that are retained in the

upper estuary were more abundant on neap rather than spring tides, possibly because they remain low in the water column to prevent being swept downstream. Samples were collected immediately after the tide stopped ebbing, so that retained zooplankters still may have been near the substrate. On the other hand, zoeae that are exported from the estuary were just as abundant on diurnal neap as spring tides. Because zooplankters were more concentrated on neap tides and at the upstream site, fishes generally preyed upon greater numbers of zooplankton on neap tides at the upstream site. More zooplankters were consumed on neap tides despite the fact that only 40% of fishes were collected on neap tides.

More zooplankton also may have been preyed upon at the upstream location because greater numbers of small fishes and fewer large fishes were collected there, as has been found in other surveys (see above for references). Small fishes were primarily zooplanktivorous, whereas large fishes preyed less upon zooplankton and more upon fish larvae, shrimps, and flying insects. The higher electivities for most zooplankters and lower electivity for "others" at the upstream site reflects the great abundance of small fishes occurring there. The electivities of fishes generally were not different between neap and spring tides because the size composition of the fish assemblage probably did not change from one lunar phase to the next (Roessler, 1970).

Thus, considerable predation pressure is being exerted

by small zooplanktivorous fishes in shallow, low-salinity, marshes of the upper estuary. Zoeae that are most susceptible to predation could have been selected to disperse into river channels and downstream where large fish predominate. Indeed, only first instar zoeae of Uca and S. cinereum were present in the upper estuary, indicating that they disperse downstream into the lower estuary and nearshore coastal waters as found in other surveys (Pinschmidt, 1963; Dudley and Judy, 1971; Sandifer, 1973; Christy and Stancyk, 1982; Truesdale and Andryszak, 1983; Brookins and Epifanio, 1985). Furthermore, Uca and S. cinereum were the only zoeae preferred by small fishes and the two most preferred zoeae by all sizes of fishes combined. Thus, it appears that Uca and S. cinereum zoeae undergo extensive horizontal migrations from the upper estuary to coastal waters which reduces their probability of encountering fish predators.

Alternatively, all zoeal instars of R. harrisii, S. reticulatum, and Palaemonetes were present in the upper estuary indicating that they are being retained there. Other surveys also have determined that R. harrisii, S. reticulatum and Palaemonetes zoeae are retained in the estuary (Pinschmidt, 1963; Williams, 1971; Sandifer, 1973; Cronin, 1982). These zoeae were the least preferred zooplankters in the upper estuary (for which electivities were calculated). Thus, zoeae that are retained in estuaries probably have evolved morphological and postcontact behavioral antipredatory adaptations to coexist with small

fishes which abound in the upper estuary.

Fish Predation and Vertical Migration

Crab zoeae did not diurnally vertically migrate as did copepods. Copepods were the most preferred prey of fishes, and therefore may be under strong selection to avoid illuminated waters. The armor of zoeae render them less vulnerable to fish predation than are copepods and they may be less constrained to remain in bottom waters during the day. In fact, tidal vertical migrations are stronger than diurnal vertical migrations by zoeae (Cronin, 1982), which may indicate that they are freer to regulate their position in the estuary during the day than copepods. Furthermore, vulnerable species of zoeae apparently make more prounounced diurnal vertical migrations than do well-armed zoeae (DeCoursey, 1976; Cronin, 1982; Brookins and Epifanio, 1985). Exported zoeae remain in well-lighted, seaward-flowing surface waters to be exported, but are particularly vulnerable to fish predation. Thus, selection has favored tidal migrations as well as migrations by zoeae into deeper waters during the day, although it is apparently more important for zoeae to expedite transport from the estuary then to remain in darkness.

Retained zoeae fluctuate between outgoing surface waters and landward flowing bottom waters which prevents flushing from estuaries, and so display much stonger tidal than diurnal vertical migration rhythms (Cronin, 1982; Forward, 1985). Retained zoeae must migrate into illumin-

ated waters on diurnal flood tides to maintain their position in the estuary, and so may be exposed to intense predation by fishes. Thus, very effective antipredatory adaptations may have been selected to deter predation by the great abundance of fishes residing in the upper estuary as zoeae migrate tidally.

Fish Predation and Hatching Rhythms

Crabs hatch nocturnally, presumably allowing zoeae a chance to disperse before being subjected to fish predation. Fishes did not appear to feed nocturnally, because undigested prey were rarely found in stomachs of fishes collected at night. However, digested prey were often present in fish midguts collected at night, because collections were usually taken several hours after nightfall. Silversides still had identifiable prey in their stomachs and/or midguts between 3.5-5 h after being fed in the laboratory. Similar evacuation rates for silversides were obtained by Peters et al. (1974), so that prey identified from guts of fishes collected from the field were probably captured before dark. Furthermore, the numbers of zooplankters present in guts of fishes collected at night were never greater than during the day. Finally, 22 specimens of all three species collected at 0130 on full moon had empty stomachs. Fundulus heteroclitus has previously been found to feed primarily in the day (Weisberg et al., 1981), and a close relative of M. menidia, M. beryllina, only feeds on zooplankton diurnally (Drenner and McComas, 1980); Wurtsbaugh and Li, 1985).

Thus, zoeae hatched nocturnally appeared to be safe from fish predation.

Semiterrestrial crabs may have been selected to release their zoeae on nocturnal spring high tides when the water volume is greatest in the upper estuary so that they are most quickly and efficiently dispersed from tidal creeks to river channels and down the estuary before sunrise to avoid predation. Semiterrestrial crabs aggregate along tidal creeks to feed on sediments rich in organics (Whiting and Moroshi, 1974), and zoeae are frequently released into these creeks. The mean number of first instar Uca zoeae per $m^3$ collected from a tidal creek on full moon was a remarkable 48,925, but only 17,281 a short distance downstream in the river channel. Saigusa (1981) demonstrated that corks released on neap tides often were stranded in tidal creeks, but those released on spring tides were carried to the mouth of the estuary. Uca and S. cinereum zoeae were most abundant on nocturnal spring tides indicating that most crabs hatch then, but by the following day the numbers of zoeae in the river channel were not significantly different than on neap tides. Consequently, similar numbers of these zoeae were preyed upon by fishes on neap and spring tides. Thus most zoeae were swept downstream before daylight, and were not subjected to predation by the great abundance of fishes occurring in the upper estuary.

Fishes and invertebrates are most abundant in shoal waters and tidal creeks and less abundant in the river

channel during summer (Springer and Woodburn, 1960; Pearcy and Richards, 1962; McErlean, 1972; Subrahmanyam and Drake, 1975; Markle, 1976; Weinstein, 1979; Crabtree and Dean, 1982; Boesch and Taylor, 1984; Fulton, 1985). Fishes and shrimps, which are also visual predators and actively select zoeae (Morgan, 1987b), occurred at densities greater than $5000/m^2$ on low ebb tides in tidal creeks (Kneib, 1984), and may decimate zoeae stranded in tidal pools.

Subtidal crabs release larvae in the main river channel (Salmon et al., 1986), and thereby are unlikely to become stranded with fishes in tidal creeks. Consequently, most subtidal crabs may not hatch synchronously about spring high tides. However, many subtidal crabs hatch on nocturnal high tides of any amplitude provided they do not occur close to sunrise (Forward et al., 1986; Salmon et al., 1986). However, if high tides do not occur soon after sunset crabs will hatch anyway to maximize the time for dispersal prior to the onset of feeding by diurnal planktivorous fishes.

Synchronized hatching by semiterrestrial crabs with vulnerable zoeae may also swamp predators as zoeae disperse from tidal creeks. The electivities of fishes for Uca zoeae were greater on spring than neap tides because more zoeae were present, but the number of zoeae consumed was not significantly different, indicating that predator swamping may have occurred. However, predator swamping would not seem to be an effective mechanism to deter fish predation, because fishes prefer the most abundant prey (Werner and

Hall, 1974; Murdoch et al., 1975; Bohl, 1982; Magnhagen, 1985). Indeed, predator swamping might be most effective for less preferred species of zoeae, because predators quickly learn to recognize and avoid noxious prey at high densities (Bohl, 1982; Dill, 1983; Bronmark et al., 1984). However, the least preferred zoeae, R. harrisii, does not hatch synchronously.

Fish Predation and Abbreviated Development

The frequency of abbreviated development increases in low salinities. Crabs that have abbreviated development frequently produce fewer, larger eggs which hatch larger larvae with shorter development times, e.g., S. reticulatum versus S. cinereum (Costlow et al., 1960; Costlow and Bookhout, 1962; Seiple, 1979). By allocating more resources per egg, crabs with abbreviated development produce large zoeae with short planktonic durations, and thus reduce the probability of fish predation and downstream transport. Alternatively, species that also range from low to high salinity areas of the estuary, but do not have abbreviated development (e.g., U. minax, U. pugnax and U. pugilator), produce zoeae which are indistinguishable morphologically. The estuarine gradient in fish predation pressure is not reflected in the reproductive and larval morphology of Uca, because larvae of all three species are exported from the estuary and are not subjected to prolonged exposure to abundant estuarine fish populations.

# CONCLUSIONS

This study suggests that predation pressure exerted by planktivorous fishes is predictable in time and space, and the reproduction, hatching rhythms, dispersal patterns, and larval morphologies of estuarine crabs have evolved together to reduce the risk of of planktivory regardless of the life history pattern exhibited. Planktivory by fishes is greatest during the day on neap tides in shallow, narrow, marshy areas of the upper estuary where productivity is high and the abundance of young fishes is great. Thus, estuarine crabs hatch early in the evening maximizing time for dispersal before sunrise. Most crabs hatch on high tides or spring high tides to dilute larvae in the greatest volume of water and increase the rapidity of initial downstream transport.

Species that are retained in the estuary producing few, large, well protected zoeae with short development times, which increases the chances of surviving encounters with fishes and reduces the risk of being transported downstream into inappropriate habitats for adult development. Alternatively, species with the most vulnerable larvae undergo more pronounced vertical migrations and extensive horizontal migrations into coastal waters, thereby diminishing the probability of encountering predators. Zoeae undertaking these long migrations must have long development times, and will derive most of their nutrition from the plankton rather than the parent. Therefore, females can invest less energy

per larva, produce more larvae per brood, brood larvae for shorter periods of time, and produce more broods than crabs retaining zoeae in the estuary. Producing more larvae per amount of energy invested will increase the probability that offspring will return to an appropriate habitat for adult development.

Large estuarine crabs may be able to employ either type of life history pattern. However, small crabs probably are constrained to retain zoeae within the estuary because they cannot produce enough small zoeae to survive a long planktonic existence and to return to a suitable adult habitat.

To understand population and community dynamics of marine systems, investigations must examine both phases of the complex life cycle because presumably they have evolved in concert. Methodological difficulties have deterred investigations on hatching rhythms and dispersal patterns of marine organisms, but they are as critical as recruitment in determining the reproductive success of an individual and the structure of marine communities.

# LITERATURE CITED

Bell, S. S., M. C. Watzin and B. C. Coull. 1978. Biogenic structure and its effect on the spatial heterogeneity of meiofauna in a salt marsh. J. Exp. Mar. Biol. Ecol. 35: 141-148.

Bengston, D. A. 1984. Resource partitioning by Menidia menidida and Menidia beryllina (Osteichtheyes: Atherinidae). Mar. Ecol. Prog. Ser. 18: 21-30.

Bireley, L. E. 1984. Multivariate analysis of species composition of shore-zone fish assemblages found in Long Island Sound. Estuaries 7: 242-247.

Blaxter, J. H. S. 1968. Visual thresholds and spectral sensitivity of herring larvae. J. Exp. Biol. 48: 39-53.

Blouw, D. M. and D. W. Hagen. 1984. The adaptive significance of dorsal spine variation in the fourspine stickleback, Apeltes quadracus. II. Phenotype-environment correlations. Can. J. Zool. 62: 1340-1350.

Boesch, D. F. and R. E. Turner. 1984. Dependence of fishery species on salt marshes: the role of food and refuge. Estuaries 7: 460-468.

Bohl, E. 1980. Diel pattern of pelagic distribution and feeding in planktivorous fish. Oecologia 44: 368-375.

Bohl, E. 1982. Food supply and prey selection in planktivorous Cyprinidae. Oecologia 134-138.

Bousfield, E. L. 1955. Ecological control of the occurrence of barnacles in the Miramichi estuary. Nat. Bus. Can. Bull. 137, Biol. Ser. 46.

Braum, E. 1967. The survival of fish larvae with reference to their feeding behavior and the food supply. In: Gerking, S. D. (ed.), The Biological Basis of Freshwater Fish Production, Blackwell Sci. Publ., Oxford, pp. 113-131.

Briggs, P. T. 1975. Shore-zone fishes of the vicinity of Fire Island inlet Great South Bay, New York. N. Y. Fish Game J. 22: 1-12.

Briggs, P. T. and O'Connor, J. S. 1971. Comparison of shore-zone fishes over naturally vegetated and sand-filled bottom in Great South Bay, N. Y. Fish Game J. 18: 15-41.

Bronmark, C., B. Malmqvist and C. Otto. 1984. Anti-predator adaptations in a neustonic insect. Oecologia 61: 189-191.

Brookins, K. G. and C. E. Epifanio. 1985. Abundance of brachyuran larvae in a small coastal inlet over six consecutive tidal cycles. Estuaries 8: 60-67.

Butner, A. and B. H. Brattstrom. 1960. Local movements in Menidia and Fundulus. Copeia 1960: 139-141.

Cain, R. L. and J. M. Dean. 1976. Annual occurrence, abundance and diversity of fish in a South Carolina intertidal creek. Mar. Biol. 36: 369-379.

Carr, W. E. S. and C. A. Adams. 1973. Food habits of juvenile marine fishes occupying seagrass beds in the estuarine zoea near Crystal River, Florida. Trans. Amer. Fish. Soc. 102: 511-540.

Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology 64: 1297-1304.

Christy, J. H. 1982. Adaptive significance of semilunar cycles of larval release in fiddler crabs (Genus Uca): test of an hypothesis. Biol. Bull. 163: 251-263.

Christy, J. H. and S. E. Stancyk. 1982. Timing of larval production and flux of invertebrate larvae in a well-mixed estuary. In: Estuarine Comparisons. V. Kennedy (ed.), Academic Press, NY, p. 489-503.

Conover, D. O. and M. R. Ross. 1982. Patterns in seasonal abundance, growth, and biomass of the Atlantic silverside in a New England estuary. Estuaries 5: 275-286.

Costlow, J. D., Jr. and C. G. Bookhout. 1962. The larval development of Sesarma reticulatum Say reared in the laboratory. Crustaceana 4: 291-294.

Costlow, J. D., Jr., C. G. Bookhout and R. Monroe. 1966. The larval development of Sesarma cinereum (Bosc) reared in the laboratory. Biol. Bull. Mar. Biol. Lab., Woods Hole 118: 183-202.

Crabtree, R. E. and J. M. Dean. 1982. The structure of two South Carolina estuarine tide pool fish assemblages. Estuaries 5: 2-9.

Croker, R. A. 1965. Planktonic fish eggs and larvae of Sandy Hook estuary. Chesapeake Sci. 6: 92-95.

Cronin, T. W. 1982. Estuarine retention of larvae of the crab Rhithropanopeus harrisii. Estuar. Coast. Shelf

Sci. 15: 207-220.

Curley, J. R., R. P. Lawton, J. M. Hickey, and J. D. Fiske. 1971. A study of the marine resources of the Waquoit Bay-eel pond estuary. Div. Mar. Fish., Dept. Nat. Res. Commonwealth Mass. Monogr. Ser. 9: 1-40.

Darnell, R. M. 1958. Food habits of fishes and larger invertebrates of Lake Pontchartrain, Louisiana, an estuarine community. Publ. Inst. Mar. Sci. Univ. Tex. 5: 353-416.

DeCoursey, P. J. 1976. Vertical migration of larval Uca in a shallow estuary. Amer. Zool. 15: 244 (Abstract).

Dill, L. M. 1983. Adaptive flexibility in the foraging behavior of fishes. Can. J. Fish. Aquat. Sci. 40: 398-408.

Dovel, W. L. 1967. Fish eggs and larvae of the Magothy River, Maryland. Chesapeake Sci. 8: 125-129.

Drenner, R. W. and S. R. McComas. 1980. The roles of zooplankter escape ability and fish size selectivity in the selective feeding and impact of planktivorous fish. In: Ecology and Evolution of Zooplankton Communities. Kerfoot, W. C. (ed.), University Press of New England, Hanover, pp. 509-517.

Dudley, D. L. and M. H. Judy. 1971. Occurrence of larval, juvenile, and mature crabs in the vicinity of Beaufort Inlet, North Carolina. NOAA Tech. Rep. NMFS SSRF-637: 1-10.

Durbin, A. G. 1979. Food selection by plankton feeding

fishes. In: Clepper, M. (ed.), International Symposium on Predator-Prey Systems in Fish Communities and Their Role in Fisheries Management. Atlanta, Georgia, July 24-27, 1978. Sport Fishing Institute, Washington, D. C., 4: 203-218.

Ferguson, R. L., G. W. Thayer and T. R. Rice. 1980. Marine primary producers. In: Functional Adaptations of Marine Organisms. Vernberg, J. (ed.), Academic Press, NY, pp. 9-69.

Fiske, J. D., E. E. Watson, P. G. Coates. 1966.A study of the marine resources of the North River. Div. Mar. Fish., Dept. Nat. Res., Commonwealth of Massachusetts Monogr. Ser. 3: 1-55.

Forward, R. B., Jr. 1985. Behavioral responses of larvae of the crab Rhithropanopeus harrisii (Brachyura: Xanthidae) during diel vertical migration. Mar. Biol. 90: 9-18.

Forward, R. B., Jr., J. K. Douglass and B. E. Kenney. 1986. Entrainment of the larval relaese rhythm of the crab Rhithropanopeus harrisii (Brachyura: Xanthidae) by cycles in salinity change. Mar. Biol. 90: 537-544.

Frank, K. T. and W. C. Leggett. 1983. Multispecies larval fish associations: accident or adaptation? Can. J. Fish. Aquat. Sci. 40: 754-762.

Fulton, R. S., III. 1984. Predation, production and the organization of an estuarine copepod community. J. Plankton Res. 6: 399-415.

Fulton, R. S., III. 1985. Predator-prey relationships in an estuarine littoral copepod community. Ecology 66: 21-29.

Gliwicz, Z. M. 1986. A lunar cycle in zooplankton. Ecology 67: 883-898.

Grant, J. W. G. and I. A. E. Bayly. 1981. Predator induction of crests in morphs of the Daphnia carinata King complex. Limnol. Oceanogr. 26: 201-218.

Grossman, G. D. 1980. Ecological aspects of ontogenetic shifts in prey size utilitization in the bay goby (Pisces: Gobiidae). Oecologia 47: 233-238.

Herman, S. S. 1963. Planktonic fish eggs and larvae of Narragansett Bay. Limnol. Oceanogr. 8: 103-109.

Hillman, R. E., N. W. Davis, and J. Wennemer. 1977. Abundance, diversity, and stability in shore-zone fish communities in an area of Long Island Sond affected by the thermal discharge of a nuclear power station. Estuar. Coast. Mar. Sci. 5: 355-381.

Hinshaw, J. M. 1985. Effects of illumination and prey contrast on survival and growth of larval yellow perch Perca flavescens. Trans. Amer. Fish. Soc. 114: 540-545.

Hobson, E. S. and J. R. Chess. 1978. Trophic relationships among fishes and plankton in the lagoon at Enewetak atoll, Marshall Islands. Fish. Bull. 76: 133-153.

Hoekstra, D. and J. Janssen. 1985. Non-visual feeding behavior of the mottled sculpin, Cottus bairdi, in Lake Michigan. Env. Biol. Fish. 12: 111-117.

Hoff, J. G. and R. M. Ibara. 1977. Factors affecting the seasonal abundance, composition and diversity of fishes in a southeastern New England estuary. Estuar. Coast. Mar. Sci. 5: 665-678.

Hunter, J. R. 1980. The feeding behavior and ecology of marine fish larvae. In: J. E. Bardach (ed.) The Physiological and Behavioral Manipulation of Food Fish as Production and Management Tools, pp. 287-330.

Hyle, R. A., II. 1976. Fishes of the Newport River estuary, North Carolina, their composition, seasonality and community structure. Ph.D. Dissertation, University of North Carolina-Chapel Hill, 192 pp.

Jacob, S. S., N. B. Nair and N K. Balasubamanian. 1983. Influence of ceratain environmental factors on the predatory efficiency of the larvivorous fish Macropodus cupanus. Env. Biol. Fish. 9: 295-300.

Judy, M. H. 1982. Catch composition, seasonality, and distribution of icthyoplankton from R/V Onslow Bay monthly cruises in Onslow Bay and Newport River estuary, North Carolina, 1972-1974. NOAA Tech. Mem. NMFS-SEFC-46, 10 pp.

Johannes, R. E. 1978. Reproductive strategies of coastal marine fishes in the tropics. Env. Biol. Fish. 3: 65-84.

June, F. C. and F. T. Carlson. 1971. Food of young Atlantic menhaden Brevoortia tyranus, in relation to metamorphosis. Fish. Bull., U.S. 68: 493-512.

Kawamura, G. and S. Hara. 1980. On the visual feeding of milkfish larvae and juveniles in captivity. Bull. Jap. Soc. Sci. Fish. 46: 1297-1300.

Kjelson, M. A., D. S. Peters, G. W. Thayer, and G. N. Johnson. 1975. The general feeding ecology of postlarval fishes in the Neport River estuary. Fish. Bull. 73: 137-144.

Kneib, R. T. 1984a. Patterns in the utilization of the intertidal salt marsh by larvae and juveniles of Fundulus heteroclitus (Linneaus) and Fundulus luciae (Baird). J. Exp. Mar. Biol. Ecol. 83: 41-51.

Kneib, R. T. 1984b. Patterns of invertebrate distribution and abundance in the intertidal salt marsh: causes and questions. Estuaries 7: 392-412.

Kneib, R. T. 1986. The role of Fundulus heteroclitus in salt marsh tropic dynamics. Amer. Zool. 26: 259-269.

Kneib, R. T. and A. E. Stiven. 1978. Growth, reproduction, and feeding of Fundulus heteroclitus (L.) on a North Carolina salt marsh. J. Exp. Mar. Biol. Ecol. 31: 121-140.

Kohler, C. C. and J. J. Ney. 1982. A comparison of methods for quantitative analysis of feeding selection of fishes. Env. Biol. Fish. 7: 363-368.

Lampert, R. and C. E. Epifanio. 1982. A comparison of dispersal strategies in two genera of brachyuran crab in a secondary estuary. Estuaries 5: 182-188.

Lechowicz, M. J. 1982. The sampling characteristics of

electivity indices. Oecologia 52: 22-30.

Lucas, J. R. 1982. Feeding ecology of the gulf silverside, Menidia peninsulae, near Crystal River, Florida, with notes on its life history. Estuaries 5: 138-144.

Magnahagen, C. 1985. Random prey capture or active choice? An experimental study on prey size selection in three marine fish species. Oikos 45; 206-216.

Magnan, P. and G. J. FitzGerald. 1984. Ontogenetic changes in diel activity, food habits and spatial distribution of juvenile and adult creek chub, Semotilus atromaculatus. Env. Biol. Fish. 11: 301-307.

Malone, T. C. 1977. Plankton systematics and distribution. MESA New York Bight Atlas Monograph 13, New York Sea Grant Institute, Albany, 41 pp.

McErlean, A. J., S. G. O'Conner, J. A. Mihursky and C. I. Gibson. 1972. Abundance, diversity and seasonal patterns of estuarine fish populations. Estuar. Coastal Mar. Sci. 1: 19-36.

Markle, D. F. 1976. The seasonality of availability and movements of fishes in the channel of the York River, Virginia. Chesapeake Sci. 17: 50-55.

Meredith, W. H. and V. A. Lotrich. 1979. Production dynamics of a tidal creek population of Fundulus heteroclitus (Linneaus). Estuar. Coast. Mar. Sci. 8:99-108.

Morgan, S. G. 1987a. Behavioral and morphological antipredatory adaptations of decapod zoeae. Oecologia.

Morgan, S. G. 1987b. The impact of planktivorous fishes on

the life histories of estuarine crabs. Ecology.

Morgan, S. G. 1987c. Selection for spination of estuarine crab zoeae versus freshwater zooplankton. Ecol. Monogr.

Mulkana, M. S. 1966. The growth and feeding habits of juvenile fishes in two Rhode Island estuaries. Gulf Res. Rep. 2: 97-168.

Murdoch, W. W., S. Avery and M. E. B. Smyth. 1975. Switching in predatory fish. Ecology 56: 1094-1105.

Nixon, S. and C. A. Oviatt. 1973. Ecology of a New England salt marsh. Ecol. Monogr. 43: 463-498.

Orth, R. J. and K. L. Heck, Jr. 1980. Structural components of eelgrass (Zostera marina) meadows in the lower Chesapeake Bay - fishes. Estuaries 3: 278-288.

Oviatt, C. A. and S. W. Nixon. 1973. The demersal fish of Narragansett Bay: an analysis of community structure, distribution and abundance. Estuar. Coast. Mar. Sci. 1: 361-378.

Paul, A. J. 1983. Light, temperature, nauplii concentrations, and prey capture by first feeding pollock larvae Theragra chalcogramma. Mar. Ecol. Prog. Ser. 13: 175-179.

Pearcy, W. G. and S. W. Richards. 1962. Distribution and ecology of fishes of the Mystic River estuary, Connecticut. Ecology 43: 248-259.

Pearson, J. C. 1941. The young of some marine fishes taken in lower Chesapeake Bay, Virginia, with special reference to the gray sea trout Cynoscion regalis. U.

S. Fish Wildl. Ser., Fishery Bull. 50: 79-102.

Penczak, T. 1985. Trophic ecology and fecundity of Fundulus heteroclitus in Chezzetcook Inlet, Nova Scotia. Mar. Biol. 89: 235-243.

Peters, D. S., M. A. Kjelson and M. T. Boyd. 1974. The effect of temperature on food evacuation rate in the pinfish (Lagodon rhomboides), spot (Leiostomus xanthurus) and silverside (Menidia menidia). Proc. 26th Ann Conf. Southeastern Assoc. Game and Fish Commissioners, 1972: 637-643.

Pinschmidt, W. C. 1963. Distribution of crab larvae in relation to some environmental conditions in the Newport River estuary, North Carolina. Ph.D. dissertation, Department of Zoology, Duke University, Durham, N. C., 112 pp.

Rajasilta, M. and I. Vuorinen. 1983. A field study of prey selection in planktivorous fish larvae. Oecologia 59: 65-68.

Richards, C. E. and M. Castagna. 1970. Marine fishes of Virginia's eastern (shore inlet and marsh, seaside waters). Chesapeake Sci. 11: 235-248.

Richards, S. W. 1959. VI. Pelagic fish eggs and larvae of Long Island Sound. Bull. Bingham Oceanogr. Coll. 17: 95-124.

Roessler, M. A. 1970. Checklist of fishes in Buttonwood Canal, Everglades National Park, Florida, and observations on the seasonal occurrrence and life histories of

selected species. Bull. Mar. Sci. 20: 860-893.

Rozas, L. P. and C. T. Hackney. 1984. Use of oligohaline marshes by fishes and macrofaunal crustaceans in North Carolina. Estuaries 7: 213-214.

Ryther, J. H. 1959. Potential productivity of the sea. Science 130: 602-608.

Saigusa, M. 1981. Adaptive significance of a semilunar rhythm in the terrestrial crab Sesarma. Biol. Bull. 160: 311-321.

Salmon, M., W. H. Seiple and S. G. Morgan. 1986. Hatching rhythms of fiddler crabs and associated species at Beaufort, North Carolina. J. Crust. Biol. 6: 24-36.

Sandifer, P. A. 1973. Distribution and abundance of decapod crustacean larvae in the York River estuary and adjacent lower Chesapeake Bay, Virginia, 1968-1969. Chesapeake Sci. 14: 235-257.

Sandifer, P. A. 1975. The role of pelagic larvae in recruitment to populations of adult decapod crustaceans in the York River estuary and adjacent lower Chesapeake Bay, Virginia. Estuar. Coast. Shelf Sci. 3: 269-279.

Sedberry, G. R. and R. F. Van Dolah. 1984. Demersal fish assemblages associated with hard bottom habitat in the South Atlantic Bight of the U.S.A. Envir. Biol. Fish. 11: 241-258.

Seiple, W. 1979. Distribution, habitat preferences and breeding periods in the crustaceans Sesarma cinereum and S. reticulatum (Brachyura: Decapoda: Grapsidae).

Mar. Biol. 52: 77-86.

Shenker, J. M. and J. M. Dean. 1979. The utilization of an intertidal salt marsh creek by larval and juvenile fishes: Abundance, diversity and temporal variation. Estuaries 2: 154-163.

Spight, T. M. 1981. Larvae of benthic invertebrates as prey of fish. Ecosynthesis 1: 125-137.

Springer, V. G. and A. J. McErlean. 1962. Seasonality of fishes on a south Florida shore. Bull Mar. Sci. Gulf Carib. 12: 39-60.

Springer, V. G. and K. D. Woodburn. 1960. An ecological study of the fishes of the Tampa Bay area. Florida State Bd. Conserv., Prof. Pap. Ser. 1, 104 pp.

Subrahmanyam, C. B. and S. H. Drake. 1975. Studies on the animal communities in two north Florida salt marshes. Bull. Mar. Sci. 25: 445-465.

Tagatz, M. E. 1968. Biology of the blue crab, Callinectes sapidus Rathbun, in the St. John's River, Florida. Fish. Bull. 67: 17-33.

Talbot, C. W. and K. W. Able. 1984. Composition and distribution of larval fishes in New Jersey high marshes. Estuaries 7: 434-443.

Targett, T. E. and J. D. McCleave. 1974. Summmer abundance of fishes in a Maine tidal cove with special reference to temperature. Trans. Amer. Fish. Soc. 1974: 325-330.

Thayer, G. W., D. E. Hoss, M. A. Kjelson, W. F. Hettler, Jr., and M. W. Lacroix. 1974. Biomass of zooplankton in

the Newport River estuary and the influence of post-larval fishes. Chesapeake Sci. 15: 9-16.

Townsend, C. R. and A. J. Risebrow. 1982. the influence of light level on the functional response of a zooplnkton-ivorous fish. Oecologia 53; 293-295.

Truesdale, F. M. and B. L. Andryszak. 1983. Occurrence and distribution of reptant decapod crustacean larvae in neritic Louisiana waters: July 1976. Contr. Mar. Sci. 26: 37-53.

Turner, J. T. 1984. The feeding ecology of some zooplankters that are important prey items of larval fish. NOAA Tech. Rep. NMFS 7: 1-28.

Turner, W. R. and G. N. Johnson. 1973. Distribution and relative abundance of fishes in Newport River, North Carolina. NOAA Tech. Rep. NMFS SSRF-666, 23 pp.

Valiela, I., J. E. Wright, J. M Teal and S. B. Volkmann. 1977. Growth, production and energy transformations in the salt-marsh killifish Fundulus heteroclitus. Mar. Biol. 66: 307-310.

Van Guelpen, L., D. F. Markle and D. J. Duggan. 1982. An evaluation of accuracy, precision, and speed of several zooplankton subsampling techniques. J. Cons. Int. Explor. Mer 40: 226-236.

Vinyard, G. L. 1980. Differential prey vulnerability and predator selectivity: effects of evasive prey on bluegill (Lepomis macrochirus) and pumpkinseed (L. gibbosus) predation. Can. J. Fish. Aquat. Sci. 37:

2294-2299.

Warfel, H. E. and D. Merriman. 1944. Studies on the marine resources of southern New England. I. Analysis of the fish population of the shore zone. 9: 1-91.

Wenner, C. A., C. A. Barans, B. W. Stender, and F. H. Berry. 1979. Results of MARMAP otter trawl investigations in the South Atlantic Bight. III. summer 1974. South Carolina Mar. Res. Dept., Tech. Rep. Ser. 41, 50 pp.

Weisberg, S. B., R. Whalen and V. A. Lotrich. 1981. Tidal and diurnal inflence on food consumption of a salt marsh killifish Fundulus heteroclitus. Mar. Biol. 61: 243-246.

Werner, E. E. and D. J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (Lepomis macrochrius). Ecology 55: 1042-1052.

Wheatland, S. B. 1956. Oceanography of Long Island Sound, 1952-1954. VII. Pelagic fish eggs and larvae. Bull. Bingham Oceanogr. Coll. 15: 234-314.

Whiting, N. H. and G. A. Moroshi. 1974. Certain organism-substrate relationships affecting the distibution of Uca minax (Crustacea: Decapoda). Hydrobiologia 44: 481-493.

Williams, A. B. 1971. A ten-year study of the meroplankton in North Carolina estuaries: annual occurrence of some brachyuran developmental stages. Chesapeake Sci. 12: 53-61.

Wurtsbaugh, W. and H. Li. 1985. Diel migrations of a

zooplanktivorous fish (Menidia beryllina) in relation to the distribution of its prey in a large eutrophic lake. Limnol. Oceanogr. 30: 565-576.

Zaret, T. M. 1980. Predation and freshwater communities. Yale University Press, New Haven, 187 pp.

Zaret, T. M. and J. S. Suffern. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. Limnol. Oceanog. 21: 804-813.

# CHAPTER 5

# SELECTION BY PLANKTONIC AND BENTHIC INVERTEBRATES FOR THE DISPERSAL PATTERNS OF ESTUARINE CRAB LARVAE

## ABSTRACT

Some species of estuarine crab larvae may migrate to nearshore coastal waters to reduce the probability of encountering planktivorous invertebrates, whereas other species of crab larvae with well developed defenses may be retained in the estuary. This hypothesis will be supported if exported species of zoeae are morphologically more susceptible to predation by invertebrates than are retained larvae, and if predation by invertebrates is more likely to occur in estuaries than coastal waters. The ability of eleven planktonic and benthic invertebrates to prey on larvae of Uca minax, which are exported from the estuary, and larvae of Rhithropanopeus harrisii, which are retained within the estuary, was investigated in laboratory feeding trials. Two of three planktonic invertebrates tested preferred U. minax larvae to R. harrisii larvae, and four of eight benthic invertebrates preferred U. minax. None of the invertebrates preferred R. harrisii to U. minax larvae. Differences in body size, swimming speed, avoidance behavior or penetrability of the exoskeleton may account for the differential predation on the two species of larvae. A review of available literature on the abundance, distribution and food habits of estuarine and coastal invertebrates indicated that estuaries generally appear to support more potential invertebrate predators of crab larvae than do coastal waters. However, many estuarine invertebrates do not appear to prey on zoeae in the field. Gut content

analyses of potential invertebrate predators from natural populations must be performed to determine if crab larvae are eaten disproportionately to further substantiate the hypothesis.

# INTRODUCTION

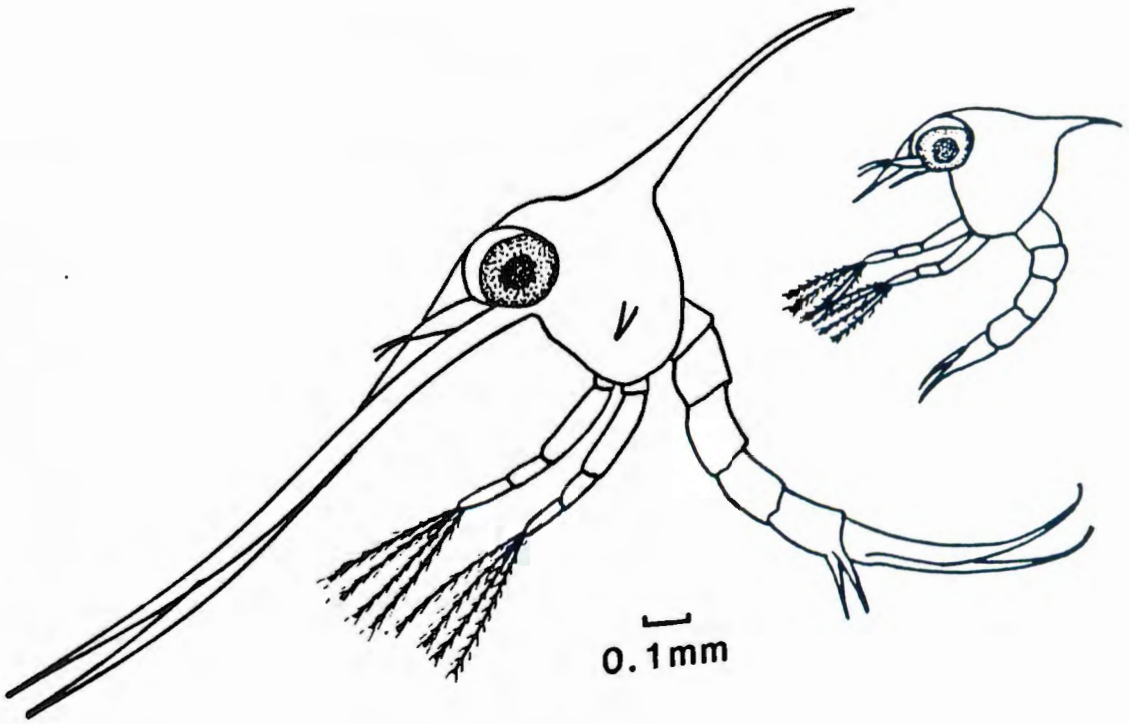
Organisms inhabiting estuaries along the east coast of the United States commonly display two dispersal patterns in which larvae are either exported from or retained within estuaries (Bousfield, 1955; Wood and Hargis, 1971; Sandifer, 1975; Goy, 1976; Weinstein et al., 1980; Christy and Stancyk, 1982; Cronin, 1982; Ouellet and Dodson, 1985). Selection could favor export of larvae from estuaries if survival or growth of larvae is greater outside the estuary where predation or physiological stress might be reduced (Christy, 1982; Strathmann, 1982). Larval export from the estuary probably has not evolved to reduce physiological stress because crab larvae that are exported survive temperature and salinity fluctuations better than do those that retain their larvae (Morgan, 1987a). However, Morgan (1987c,d) has shown that predation by planktivorous fishes, which are more abundant within the estuary than offshore, may have selected for export of vulnerable estuarine crab larvae. The smaller size and shorter spines of the exported zoeae made them more susceptible to predation by small fishes compared to the long spines and larger body size of the retained zoeae.

The greater productivity of estuaries also may support more invertebrate predators of larvae than occur offshore (Weinstein, 1979; Boesch and Turner, 1984), and could intensify selection for export of vulnerable zoeae if the same species of zoeae that are vulnerable to fish predation

also are more susceptible to predation by invertebrates. However, the elongate spines of Rhithropanopeus harrisii zoeae, which are retained in the estuary, were shown to be ineffective against nine of ten invertebrate predators (Morgan, 1987b). Invertebrate predators may not have difficulty with spines, but body size, penetrability of the exoskeleton, evasive capabilities, and encounter rates also may determine the susceptibility of zoeae to predation.

To support the hypothesis that estuarine larvae vulnerable to invertebrate predation migrate to coastal waters to avoid predation, one must demonstrate that 1) exported larvae are indeed more likely to be preyed upon by invertebrates than are retained larvae, and 2) predation by invertebrates is more likely to occur in estuaries than coastal waters. Thus, the ability of eleven planktonic and benthic invertebrates to prey on fiddler crab, Uca minax, and mud crab, R. harrisii, zoeae (Figure 1) in the laboratory was investigated to determine if fiddler crab zoeae are more susceptible to invertebrate predation than are mud crab zoeae. Both species of crabs coexist at the heads of estuaries in salinities of 0-25 o/oo. However, larvae of the semiterrestrial fiddler crab are exported from the estuary (Christy and Stancyk, 1982; Truesdale and Andryzak, 1983) whereas larvae of the subtidal mud crab have evolved behavioral mechanisms that enable them to remain in the upper estuary (Cronin, 1982; Lambert and Epifanio, 1982). Published accounts of invertebrate predation on zoeae in

Figure 1. First instar A) *R. harrisii* and B) *U. minax* zoeae.


0.1mm

natural populations, as well as the distribution and abundance of potential invertebrate predators, were reviewed to determine if invertebrate predation in estuaries is likely to be greater than in coastal waters.

## METHODS AND MATERIALS

The vulnerability of *U. minax* and *R. harrisii* larvae (Figure 1) to invertebrate predation was determined by offering larvae of each species to 11 invertebrates with different feeding modes (Table 1). Invertebrates and gravid crabs were collected from the Newport and Neuse River estuaries, North Carolina. Gravid crabs were placed singly in 19 cm culture dishes and were provided with 25 o/oo seawater. Crabs were held in incubators at 25°C and a 12 h light: 12 h dark photoperiod until eclosion. Invertebrates were placed in culture dishes and were allowed to adjust to laboratory conditions for at least one day prior to experimentation. The size of the culture dishes used as arenas for the feeding trials and the number of larvae fed in a single trial depended upon the size of the predators (Table 1). Predators were offered randomly either *U. minax* or *R. harrisii* larvae, and the number of larvae remaining after 24 h was counted. Experiments were repeated until both species of zoeae were fed to predators. All experiments were conducted at 25°C and 25 o/oo. The number of prey remaining were compared by analysis of variance.

Table 1. Mean size and minimum and maximum size (mm) of 11 planktonic and benthic invertebrate predators, diameter of culture dishes (cm) used for feeding trials, number of crab larvae fed of each species, and number of replicates. Measurements (M.): L=length, W=width, H=height, OW=operculum width, BW=base width, and TW=distance from tip of tentacle to opposing tentacle tip.

| PREDATOR | TAXON/ COMMON NAME | PREDATOR SIZE M. | MEAN | MIN.-MAX. | DISH SIZE | NO. LARVAE | N |
|---|---|---|---|---|---|---|---|
| PLANKTONIC | | | | | | | |
| *Sagitta hispida* | Chaetognath | L: | 7.5 | 7-8 | 6 | 20 | 19 |
| *Eutima mira* | Hydromedusa | W: | 5.2 | 5-8 | 6 | 20 | 15 |
| *Mnemiopsis leidyi* | Ctenophore | L: | 20.2 | 4-30 | 9,19 | 40,100 | 20 |
| BENTHIC | | | | | | | |
| *Styela plicata* | Tunicate | H: | 39.4 | 28-82 | 19 | 100 | 19 |
| | | W: | 24.0 | 13-42 | | | |
| *Aiptasia pallida* | Anemone | BW: | 9.7 | 2-17 | 9 | 40 | 15 |
| | | TW: | 25.7 | 11-50 | | | |
| *Balanus amphitrite* | Barnacle | OW: | 7.6 | 5.9-9.6 | 6 | 20 | 19 |
| | | BW: | 9.5 | 6.7-14.4 | | | |
| | | H: | 9.3 | 7.0-14.1 | | | |
| *Caprella penantis* | Amphipod | L: | 5.1 | 3-8 | 6 | 20 | 18 |
| *Palaemonetes pugio* | Grass shrimp | L: | 27.2 | 22.0-30.0 | 9 | 40 | 20 |
| *Rhithropanopeus harrisii* | Crab | W: | 9.6 | 8.7-10.8 | 9 | 40 | 20 |
| *Geukensia demissa* | Mussel | L: | 56.0 | 48-75 | 9 | 40 | 10 |
| *Crassostrea virginica* | Oyster | L: | 63.7 | 56-82 | 9 | 40 | 10 |

## RESULTS AND DISCUSSION

### Differential Preference of Invertebrates for Zoeae

The results of the invertebrate predation experiments are consistent with the hypothesis that selection for export or retention of estuarine larvae may be due to not only fish predation, but to invertebrate predation as well. Six of the 11 invertebrates preying on crab larvae in the laboratory preferred larvae that are exported from the estuary (U. minax), and none preferred the retained larvae (R. harrisii) (Figure 2, Table 2). Two of the three planktonic invertebrates (hydromedusa, chaetognath) preferred larvae that are exported from the estuary and one showed no preference (ctenophore). Four of the eight benthic invertebrates tested also preferred U. minax to R. harrisii larvae (S. plicata, A. pallida, B. amphitrite, C. virginica), and the remainder demonstrated no preference (C. penantis, P. pugio, R. harrisii, G. demissa).

Morgan (1987b) has shown that spines are generally ineffective at deterring predation by invertebrates. Therefore, differences in swimming speed, body size, avoidance behavior, or penetrability of the exoskeleton may account for the differential predation on mud and fiddler crab zoeae. Uca larvae are smaller, but swim twice as fast as R. harrisii larvae (Herrnkind, 1968; Latz and Forward, 1977). Because U. minax swim faster than R. harrisii zoeae, they would encounter more predators and would be more likely to be preyed upon, unless faster swimming also increases the

Figure 2. Mean number of surviving R. harrisii and U. minax larvae fed to 11 benthic and invertebrate predators. Significance levels: * = .05, ** = .01, *** = .001.

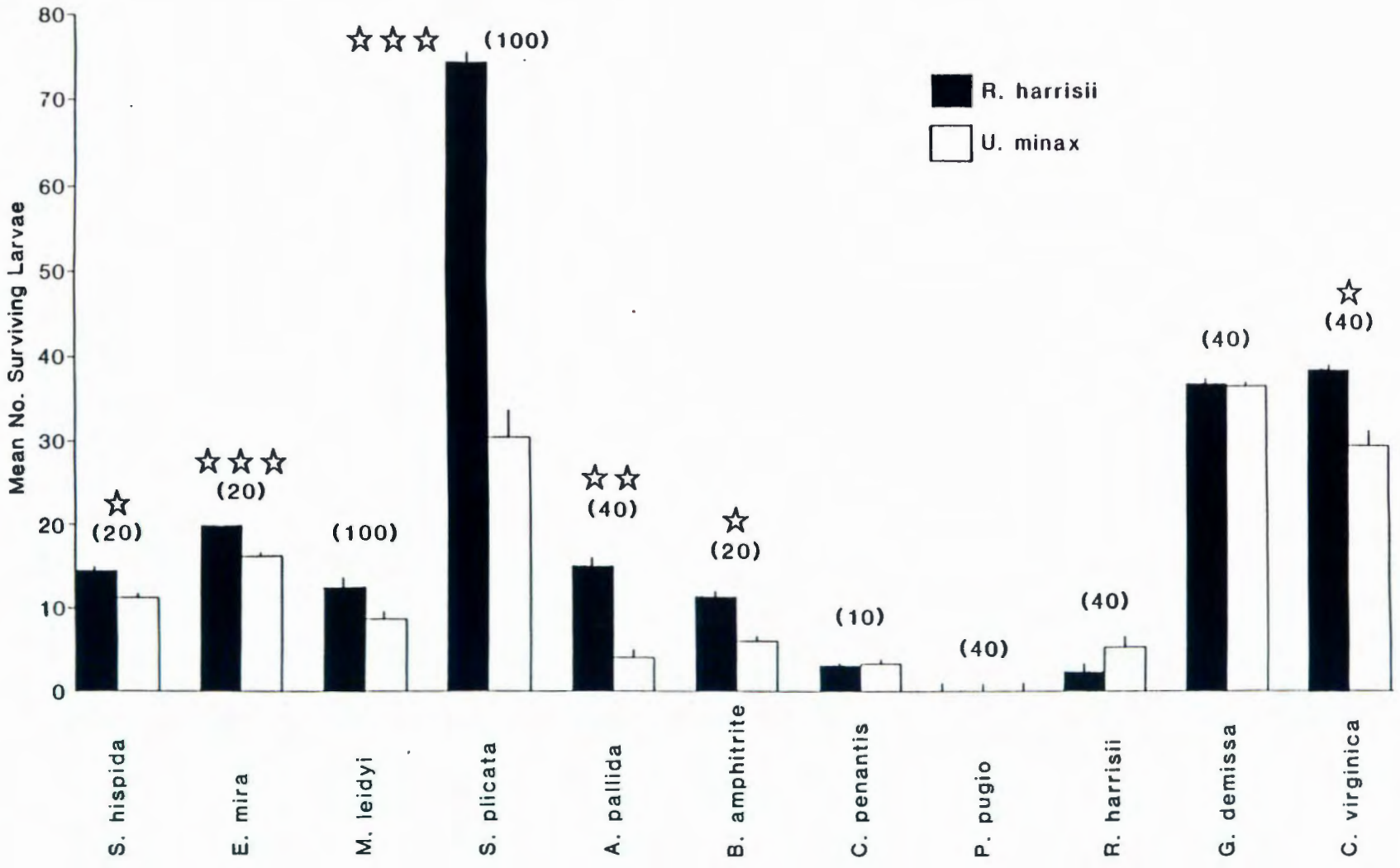

Mean No. Surviving Larvae
80
70
60
50
40
30
20
10
0
R. harrisii
U. minax
☆ (20)
☆☆☆ (20)
(100)
☆☆☆ (100)
☆☆ (40)
☆ (20)
(10)
(40)
(40)
(40)
☆ (40)
S. hispida
E. mira
M. leidyi
S. plicata
A. pallida
B. amphitrite
C. penantis
P. pugio
R. harrisii
G. demissa
C. virginica

Table 2. Analysis of variance of invertebrate predation on spined and despined *R. harrisii* larvae.

| PREDATOR | MS | F | P |
|---|---|---|---|
| *Sagitta hispida* | 79.61 | 4.31 | .045 |
| *Eutima mira* | 90.13 | 17.54 | .0003 |
| *Mnemiopsis leidyi* | 207.59 | 2.32 | .14 |
| *Styela plicata* | 18348.03 | 31.51 | .0001 |
| *Aiptasia pallida* | 886.60 | 10.89 | .003 |
| *Balanus amphitrite* | 268.45 | 5.88 | .02 |
| *Caprella penantis* | 1.00 | 0.10 | .76 |
| *Rhithropanopeus harrisii* | 87.03 | 3.33 | .08 |
| *Geukensia demissa* | 1.13 | 0.19 | .67 |
| *Crassostrea virginica* | 378.45 | 7.17 | .02 |

likelihood of escape. The large body size of R. harrisii larvae also may have made it more difficult for small predators, such as E. mira, S. hispida, and Balanus amphitrite, to capture and ingest them. The small size of the siphons of Styela plicata and Crassostrea virginica also may make it difficult to ingest large particles. There may be a critical size at which the feeding mechanisms become inefficient, so that whether or not spines of R. harrisii larvae were present the organism is already too large to be effectively preyed upon. Furthermore, if R. harrisii larvae have longer spines they also may have thicker exoskeletons than U. minax larvae, because long spines and thick protective coverings appear to be correlated in freshwater rotifers and cladocerans (Williamson, 1983; Kerfoot, 1984). If so, predators bearing nematocysts, like Aptasia pallida and E. mira, may be less able to penetrate the armor of larvae of R. harrisii than U. minax (Arkett, 1984; Fulton and Wear, 1985). The strength of the escape response also may determine whether or not zoeae can break free from hydromedusae and anemones (Fulton and Wear, 1985). Differences in predator avoidance behavior were not observed between the two species of crab zoeae.

Most of the invertebrates that did not demonstrate a preference between the two species of crab larvae (P. pugio, R. harrisii adults, Caprella penantis) use chitinous mouthparts and chelae to feed. Grass shrimp pursued zoeae and collected them with their mouthparts and their chelate

maxillipeds, and usually consumed all forty larvae within 15 min. The mud crab appeared to rely only on their mouthparts for capturing larvae. The adhesion provided by the colloblast cells of the ctenophore apparently are sufficient to capture either species of larva and carry them to the distensible coelenteron. The mussel did not appear to feed readily on either species of larva, though it does prey on smaller, weaker-swimming invertebrate larvae (Mileikovsky, 1974; Cowden et al., 1984).

To support fully the hypothesis that vulnerable larvae migrate to coastal waters to reduce predation, it must be shown not only that invertebrates prefer the exported species of zoeae but that they actually do so in the field. Furthermore, predation pressure must be shown to be greater within the estuary than in coastal waters.

Predation Pressure by Planktonic Invertebrates

The preferences for U. minax and R. harrisii by three major types of invertebrate planktonic predators (ctenophore, hydromedusa, chaetognath) coexisting at the head of the Newport River estuary with the crab populations (Morgan, 1987d) were tested. Of these, the abundant gelatinous zooplankton are most likely to have an impact on larval populations. Miller and Williams (1972) found that the total biomass of ctenophores (Mnemiopsis leidyi, Beroe ovata), hydromedusae (Nemopsis bachei) and scyphomedusae (Chrysaora quinquicirrha, Cyanea capitella, Aurelia aurita) in the Patuxent River estuary was a remarkable 23-39 $l/m^3$

during summer months when crab larvae are hatched. These authors concluded that the standing crop of zooplankton was insufficient to sustain the number of ctenophores and jellyfishes.

Decimation of estuarine zooplankton populations has been correlated with the presence of M. leidyi (Herman et al., 1968; Miller, 1970; Miller and Williams, 1972; Hulszier, 1976; Reeve and Walter, 1978; Kremer, 1979; Deason and Smayda, 1982; Turner et al., 1983; Bengston, 1984; Feigenbaum and Kelly, 1984). Mnemiopsis leidyii were so abundant in the upper Newport River estuary that they sometimes filled the cone of a plankton net. Quantitative estimates of population abundance of M. leidyi have revealed that, although the ctenophore occurs in estuarine and coastal waters less than 33 o/oo (Bigelow, 1915; Bishop, 1972), the greatest abundance in the Newport River area occurs in the upper estuary (2-23 o/oo) (Schwartz and Chestnut, 1974).

Although M. leidyi can decimate standing crops of zooplankton in the upper estuary, the impact of this predator on crab larvae is questionable. These voracious, abundant planktivores fed on crab larvae in the laboratory, but Cronin et al. (1962) and Burrell and van Engel, (1976) found that crab larvae occurred abundantly with M. leidyi but were rarely consumed. Both R. harrisii and U. minax larvae have a shadow response which enables them to avoid contact with ctenophores (Herrnkind, 1968; Forward, 1976; Forward, 1986). However, once contact is made, laboratory

results in the present study indicate that both R. harrisii and U. minax are readily preyed upon. The other abundant estuarine ctenophore, B. ovata, occurring in estuaries feeds primarily on other ctenophores (Swanberg, 1974). Although less abundant than estuarine ctenophore populations, the coastal ctenophore, Pleurobrachia pileus, also is believed to severely reduce standing crops of zooplankton (Reeve and Walter, 1978; Frank, 1986). Thus, although ctenophores exert the greatest predation pressure in the upper estuary, they apparently feed on both species of crab larvae rarely and in similar numbers, and probably are not a major selective force in the evolution of larval dispersal patterns of crabs.

Of the zooplankters quantified in the upper Newport estuary (Morgan, 1987d), the hydrozoan medusa, Eutima mira, was the fourth most abundant; only larvae of Uca spp. larvae, copepods, and barnacle nauplii were more abundant. The mean density of E. mira was 401.7/$m^3$ and it attained a maximum density of 4177.8/$m^3$. Hydromedusae also have been reported to very abundant in other estuaries (Cronin et al., 1962; Phillips et al., 1969), and may decimate standing stocks of zooplankton (Arkett, 1984; Fulton and Wear, 1985). Furthermore, hydromedusae have been shown to prey on crustacean larvae in the field (Cronin et al., 1962; Phillips et al., 1969), perhaps because the small size of E. mira may not reduce light intensity sufficiently to initiate the shadow response. Hydromedusans may exert

considerable differential pressure on the larval populations of the two crabs because they prefer U. minax to R. harrisii larvae in the laboratory, feed on crab larvae in the field, and apparently are more abundant in the upper estuary than in coastal waters.

Scyphomedusae were not found in the upper Newport River estuary (Morgan, 1987d), and their preferences for larvae were not determined. However, scyphomedusae were observed to co-occur with U. minax and R. harrisii populations in the adjacent Neuse River estuary. Scyphomedusans have been reported to prey on crab larvae (Fraser, 1969; Phillips et al., 1969). However, the sea nettle, Chrysaora quinquecirrha, is the predominant jellyfish in the upper estuary during summer months (Cargo and Schultz, 1967; Herman et al., 1968; Miller and Williams, 1972; Miller, 1974), and it feeds primarily on M. leidyi and fish larvae (Cargo and Schultz, 1967; Phillips et al., 1969). However, crustacean zooplankton can be a significant food source for C. quinquecirrha when ctenophores are absent (Kelly, 1983). Other abundant estuarine scyphomedusans include the winter jellyfish, Cyanea capillata, which preys primarily on M. leidyi (Phillips et al., 1969; Turner, 1982). The moon jellyfish, Aurelia aurita, is common during the summer in the lower estuary and coastal waters, where it feeds on copepods and fish larvae (Moller, 1980; Bailey and Batty, 1984; Feigenbaum and Kelly, 1984; van deer Veer and Oorthuysen, 1985). Thus, scyphomedusans are somewhat unlikely to

influence the evolution of dispersal patterns of estuarine crab larvae because gut content analyses have revealed that the most abundant estuarine jellyfish do not feed on crab larvae; the latter may avoid contact with jellyfish due to their shadow response.

The chaetognath, S. hispida, also preferred U. minax to R. harrisii larvae. However, S. hispida was only the 24th most abundant zooplankter in the upper Newport estuary (Morgan, 1987d). The mean density of S. hispida was 1.1/$m^3$ and it attained a maximum density of 11.2/$m^3$. Chaetognaths are transported from the continental shelf into the estuary. Consequently, densities of chaetognaths in the lower estuary and coastal waters are generally greater than those found in the upper estuary (Cronin et al., 1962; Grant, 1977). Mean densities of chaetognaths in the lower estuary are greater than 100 /$m^3$ and maximum densities can attain 800 /$m^3$ (Grant, 1977; Fulton, 1984; Tiselius and Peterson, 1986). However, even in the lower estuary chaetognaths are of minor trophic significance (Comino and Grant, 1985). Furthermore, analyses of gut contents in field populations indicate that chaetognaths feed overwhelmingly on copepods (Sullivan, 1980; Edmunds, 1983; Fulton, 1984; Comino and Grant, 1985). Although S. hispida does feed preferentially on U. minax in the laboratory, they do not appear to be an important predator of crab larvae in the field nor are they more abundant in the upper estuary than offshore. Therefore, the two dispersal patterns probably cannot be attribu-

ted to the differential predation pressures exerted by this predator alone.

In addition to chaetognaths, other zooplankters primarily or exclusively occur in coastal waters which larvae exported from the estuary may encounter. For instance, sea wasps (cubomedusae) and cabbageheads (scyphomedusae) prey on crab larvae (Phillips et al., 1969). Predaceous copepods (Lillelund and Lasker, 1971; Landry, 1978; Bailey, 1984; Turner et al., 1985), hyperiid amphipods (Westernhagen et al., 1979; Yamashita et al., 1985), euphausiids (Theilacker and Lasker, 1974; Bailey, 1984), sergestids (Omori and Gluck, 1979), and siphonphores (Purcell, 1981) all are capable of feeding on fish larvae, although it is not known if they feed on crab larvae.

Predation Pressure by Benthic Invertebrates

Larval predation by benthic invertebrates, including oysters, mussels and other bivalves, brachiopods, barnacles, hydroids, sponges, polychaetes, amphipods and pandalid shrimp can be great (see Mileikovsky, 1974 for review of early references; Ambrose, 1982; Commito, 1982; Oliver et al., 1982), although mysids do not appear to prey on larvae (Fulton, 1982). Benthic invertebrates in nature have been reported prey upon mollusc larvae, barnacle nauplii, cyprids, annelid larvae, shrimp zoeae, echinoderm larvae, and tunicate larvae, but not upon crab larvae. Mysids and anthozoans did not consume zoeae even though they were present in the plankton (Fulton, 1982; Sébens and Koehl,

1984).

Larvae are more likely to come in contact with benthic invertebrates in shallow estuaries compared to deeper coastal waters. The upper Newport River estuary is less than a meter deep at low tide and larvae could be exposed to predation by benthic invertebrates. Furthermore, the density of macroinvertebrates can be greater in the estuary than offshore. Although the biomass and numbers of benthic macroinvertebrates is greater in the lower than the upper Newport River estuary (Chester et al., 1983), their density is approximately ten times greater in the Chesapeake Bay than the inner continental shelf (Dauer et al., 1984). Also, the biomass of macroinvertebrates inhabiting hard bottoms of the inner shelf of the South Atlantic Bight is greater than on the outer shelf (Wenner et al., 1983).

The positive phototaxis of first instar U. minax larvae would maintain larvae in seaward flowing surface waters, and would minimize contact with benthic invertebrates as they are transported offshore into safer waters. Strathmann (1982) compared the instantaneous mortality rates of copepods between the benthos and plankton and between estuarine and coastal waters, and determined that the benthos is as hazardous as the plankton for zooplankton and that estuarine waters are more hazardous than coastal waters. Thus, U. minax may reduce contact with benthic invertebrates by migrating from the shallow upper estuary to the continental shelf, where the density of potential macroinverte-

brate predators would be less if they were to encounter benthic communities. Furthermore, larvae retained in the upper estuary by remaining in bottom currents may encounter less predation by macroinvertebrates than if they migrated to the lower estuary where the density of macroinvertebrates may be greater.

## CONCLUSIONS

Several findings are consistent with the hypothesis that the migrations of vulnerable larvae to coastal waters reduces predation by invertebrates as well as fishes. Most planktonic and benthic invertebrates preferred U. minax which exports its larvae, and none preferred R. harrisii larvae, which are retained in the estuary. The productivity of estuaries is generally higher than coastal waters and appears to support a greater density of potential invertebrate predators of crab larvae. Gelatinous and benthic zooplanktivores appear to be more numerous in the estuary than coastal waters, and many benthic invertebrates prey on invertebrate larvae in the field. Retained larvae must frequent bottom waters to remain in the estuary, so it is more likely that retained larvae would encounter benthic invertebrates where their density is greatest. Furthermore, instantaneous mortality rates of copepods by all predators are as great near the benthos as in the plankton, and greater in the estuary than offshore (Strathmann, 1982).

On the other hand, most estuarine planktonic predators (ctenophores, scyphomedusans and chaetognaths) do not appear

to prey on crab larvae in the field; only hydromedusans have been reported to feed on crustacean larvae in natural populations. Furthermore, there is a greater diversity of possible planktonic predators in coastal waters, although the ability of most to prey on crab larvae is unknown. Finally, I am unaware of any reports of benthic invertebrates feeding on crab larvae in the field.

Thus, although the preference by invertebrates for the exported species of larvae and the greater predation pressure of estuaries compared to coastal waters supports the hypothesis that vulnerable larvae are exported to reduce predation, there is little evidence that many invertebrates in natural populations actually prey on crab larvae. Gut content analyses of potential invertebrate predators collected from natural populations must be performed to determine if crab larvae are eaten disproportionately to substantiate further the hypothesis that the horizontal migrations of crab larvae from the estuary to coastal waters evolved to reduce invertebrate predation.

# LITERATURE CITED

Ambrose, W. G. 1984. Role of predatory infauna in structuring marine soft-bottom communities. Mar. Ecol. Progr. Ser. 17: 109-115.

Bailey, K. M. and R. S. Batty. 1983. A laboratory study of predation by Aurelia aurita on larval herring (Clupea harengus): Experimental observations compared with model predictions. Mar. Biol. 72: 295-301.

Bailey, K. M. 1984. Comparison of laboratory rates of predation on five species of marine fish larvae by three planktonic invertebrates: effects of larval size on vulnerability. Mar. Biol. 79: 303-309.

Bigelow, H. B. 1915. Exploration of the coast water between Nova Scotia and Chesapeake bay, July and August, 1913, by the U. S. Fisheries Schooner Grampus. Ocanography and plankton. Bull. Mus. Compar. Zool. 49:

Bishop, J. W. 1972. Ctenophores of the Chesapeake Bay. Chesapeake Sci. 13 (supplement): S98-S100.

Bousfield, E. L. 1955. Ecological control of occurrence of barnacles in the Miramichi estuary. Bull. Nat. Mus. Canada 137: 69.

Burrell, V. G., Jr. and Van Engel, W. A. 1976. Predation by and distribution of a ctenophore, Mnemiopsis leidyi A. Agassiz, in the York River estuary. Estuar. Coast. Mar. Sci. 4:235-242.

Canino, M. F. and G. C. Grant. 1985. The feeding and diet of Sagitta tenuis (Chaetognatha) in the lower Chesapeake

Bay. J. Plankton Res. 7(2): 175-188.

Cargo, D. G. and L. P. Schultz. 1967. Further observations on the biology of the sea nettle and jellyfishes in Chesapeake Bay. Chesapeake Sci. 8(4): 209-220.

Chester, A. J., R. L. Ferguson and G. W. Thayer. Environmental gradients and benthic macroinvertebrate distributions in a shallow North Carolina estuary. Bull. Mar. Sci. 33(2): 282-295.

Christy, J. H. 1982. Adaptive significance of semilunar cycles of larval release in fiddler crabs (genus Uca): test of an hypothesis. Biol. Bull. 163: 251-263.

Christy, J. H. and S. E. Stancyk. 1982. Timing of larval production and flux of invertebrate larvae in a well-mixed estuary. In: Estuarine Comparisons, V. Kennedy (ed.) Academic Press, Orlando, p. 489-503.

Commito, J. A. 1982. The importance of predation by infaunal polychaetes in controlling the sturcture of a soft-bottom community in Maine, USA. Mar. Biol. 68: 77-81.

Cowden, C., C. M. Young and F. S. Chia. 1984. Differential predation on marine invertebrate larvae by two benthic predators. Mar. Ecol. Progr. Ser. 14: 145-149.

Cronin, L. E., J. C. Daiber and E. M. Hulbert. 1962. Quantitative seasonal aspects of zooplankton in the Delaware River estuary. Chesapeake Sci. 3(2): 63-93.

Cronin, T. W. 1982. Estuarine retention of larvae of the crab Rhithropanopeus harrisii. Estuar. Coast. Shelf Sci. 15: 207-220.

Dauer, D. M., T. L. Stokes, Jr. H. R. Barker, Jr., R. M. Ewing and J. W. Sourbeer. 1984. Macrobenthic communities of the lower Chesapeake Bay. IV. Bay-wide transects and the inner continental shelf. Int. Revue ges. Hydrobiol. 69: 1-22.

Deason, E. E. and T. J. Smayda 1982. Ctenophore-zooplankton-phytoplankton interactions in Narrangansett Bay, Rhode Island, USA, during 1972-1977. J. Plankton Res. 4: 203-217.

Edmunds, P. J., S. M. Evans, S. Hutabarat and P. Soedarsono. 1983. Preliminary observations on predator/prey relationships between chaetognaths and copepods in the Java Sea. Mar. Behav. Physiol. 10: 97-102.

Feigenbaum, D. and M. Kelley. 1984. Changes in the lower Chesapeake bay food chain in presence of the sea nettle Chrysaora quinquecirrha (Scyphomedusae). Mar. Ecol. Progr. Ser. 19: 39-47.

Forward, R. B., Jr. 1976. A shadow response in a larval crustacean. Biol. Bull. 115: 126-140.

Forward, R. B., Jr. 1986. A reconsideration of the shadow response of a larval crustacean. Mar. Behav. Physiol. 12: 99-113.

Frank, K. T. 1986. Ecological significance of the ctenophore Pleurobrachia pileus off southwestern Nova Scotia. Can. J. Fish. Aquat. Sci. 43(1): 211-222.

Fraser, J. H. 1969. Experimental feeding of some medusae and chaetognatha. J. Fish. Res. Bd. Can. 26: 1743-1762.

Fulton, R. S., III. 1982. Predatory feeding of two marine mysids. Mar. Biol. 72: 183-191.

Fulton, R. S., III. 1984. Effects of chaetognath predation and nutrient enrichment on enclosed estuarine copepod communities. Oecologia 62: 97-101.

Gilbert, J. J. 1967. Asplanchna and posterolateral spine production in Brachionus calyciflorus. Archives Hydrobiology. 64: 1-62.

Goy, J. W. 1976. Seaonal distribution and retention of some decapod crustacean larvae within the Chesapeake Bay, Virginia. M.S. Thesis, Old Dominion University, Norfolk, VA, 334 p.

Grant, G. C. 1974. Seasonal distribution and abundance of the Chaetognatha in the lower Chesapeake Bay. Estuar. Coast. Mar. Sci. 5: 809-824.

Grant, J. W. G. and I. A. E. Bayly. 1980. Predator induction of crests in morphs of the Daphnia carinata King complex. Limnol. Oceanogr. 26(2): 201-218.

Herman, S. S., J. A. Mihursky and A. J. McErlean. 1968. Zooplankton and environmental characteristics of the Patuxent River Estuary 1963-1965. Chesapeake Sci. 7: 59-74.

Herrnkind, W. F. 1968. The breeding of Uca pugilator and mass rearing of the larva with comments on the behavior of the larvae and early crab stages. Crustaceana (supplement) 2: 214-224.

Kelly, M. G. 1983. The effect of sea nettle abundance on the

food chain of the lower Chesapeake Bay. M. A. thesis, Old Dominion University, Virginia.

Kerfoot, W. C. 1977. Implications of copepod predation. Limnol. Oceanogr. 22(2): 316-325.

Kremer, P. 1979. Predation by the ctenophore Mnemiopsis leidyi in Narragansett Bay, Rhode Island. Estuaries 2(2): 97-105.

Kuhlmann, D. 1977. Laboratory studies on the feeding behaviour of the chaetognaths Sagitta setosa J. Muller and S. elegans Verril with special reference to fish eggs and larvae as food organisms. Meeresforschung 25: 163-171.

Lambert, R. and C. E. Epifanio. 1983. Comparison of dispersal strategies in two genera of brachyuran crab in a secondary estuary. Estuaries 5: 182-188.

Landry, M. R. 1978. Predatory feeding behavior of a marine copepod, Labidocera trispinosa. Limnol. Oceanogr. 23: 1103-113.

Latz, M. I. and R. B. Forward, Jr. 1977. The effect of salinity upon phototaxis and geotaxis in a larval crustacean. Biol. Bull. 153: 163-179.

Leber, K. M., III. 1983. Feeding ecology of decapod crustaceans and the influence of vegetation on foraging success in a subtropical seagrass meadow. Ph. D. Dissertation, Florida State University, Tallahassee. 166 p.

Lebour, M. V. 1922. The food of plankton organisms. J. Mar.

Biol. Assoc. U. K. 12: 644-677.

Lebour, M. 1923. The food of plankton organisms II. J. Mar. Biol. Assoc. U. K. 13: 70-92.

Lillelund, K. and R. Lasker. 1971. Laboratory studies of predation by marine copepods on fish larvae. Fish. Bull. U. S. 69: 655-667.

Mileikovsky, S. A. 1974. On predation of pelagic larvae and early juveniles of marine bottom invertebrates by adult benthic invertebrates and their passing alive through their predators. Mar. Biol. 26: 303-311.

Miller, R. J. 1974. Distribution and biomass of an estuarine ctenophore population, Mnemiopsis leidyi (A. Agassiz). Chesapeake Sci. 15(1): 1-8.

Miller, R. J. and R. B. Williams. 1972. Energy requirements and food supplies of ctenophores and jellyfish in the Patuxent River Estuary. Chesapeake Sci. 13(4): 328-331.

Moller, H. 1984. Reduction of a larval fish population by jellyfish predator. Science 224: 621-622.

Morgan, S. G. 1987a. Selection on hatching rhythms and dispersal patterns of estuarine crab larvae: avoidance of physiological stress by larval export? J. Exp. Mar. Biol. Ecol.

Morgan, S. G. 1987b. Selection for spination of estuarine crab zoeae versus freshwater zooplankton. Ecol. Monogr.

Morgan, S. G. 1987c. Behavioral and morphological antipredatory adaptations of decapod zoeae. Oecologia.

Morgan, S. G. 1987d. The impact of planktivorous fishes on the life histories of estuarine crabs. Ecology.

O'Brien, W. J., D. Kettle and H. Riessen. 1979. Helmets and invisible armor: sturctures reducing predation from tactile and visual predators. Ecology 60(2): 287-294.

Oliver, J. S. J. M. Oakden and P. N. Slattery. 1982. Phoxocephalid amphipod crustaceans as predators on larvae and juveniles in marine soft-bottom communities. Mar. Ecol. Progr. Ser. 7: 179-184.

Omori, M. and D. Gluck. 1979. Life history and vertical migration of the pelagic shrimp Sergestes similis off the southern California coast. Fish. Bull. 77(1): 183-198.

Ouellet, P. and J. J. Dodson. 1985. Tidal exchange of anadromous rainbow smelt (Osmerus mordax) larvae between a shallow spawning tributary and the St. Lawrence estuary. Can. J. Fish. Aquat. Sci. 42(8): 1352-1358.

Pearre, S. 1973. Vertical migration and feeding in Sagitta elegans Verrill. Ecology 54: 300-314.

Pennington, J. T. and F. S. Chia. 1984. Morphological and behavioral defenses of trochophore larvae of Sabellaria cementarium (Polychaeta) against four planktonic predators. Biol. Bull. 167: 168-175.

Phillips, P. J., W. D. Burke and K. J. Keener. 1969. Observations on the trophic significance of jellyfishes in Mississippi Sound with quantitative data on the

associative behavior of small fishes with medusae. Trans. Am. Fish. Soc. 98(4): 703-712.

Purcell, J. E. 1981. Feeding ecology of Rhizophysa eysenhardti, a siphonophore predator of fish larvae. Limnol. Oceanogr. 26 (3): 424-432.

Sandifer, P. A. 1975. The role of pelagic larvae in recruitment to populations of adult decapod crustaceans in the York River estuary and adjacent lower Chesapeake Bay, Va. Estuar. Coast. Mar. Sci. 3: 269-279.

Schwartz, F. J. and A. F. Chestnut. 1974. Biological investigations of noxious coelenterates and ctenophores in coastal North Carolina North Carolina. Div. Commercial Sport Fish. Spec. Sci. Rep. 27: 1-59.

Strathmann, R. R. 1982. Selection for retention or export of larvae in estuaries. In: Estuarine Comparisons. V. Kennedy (ed.), Academic Press, Inc., NY, p. 521-536.

Sullivan, B. K. 1980. In situ feeding behavior of Sagitta elegans and Eukrohnia hamata (Chaetognatha) in relation to the vertical distribution and abundance of prey at Ocean Station "P". Limnol. Oceanogr. 25(2): 317-326.

Sullivan, B. K. and M. R. Reeve. 1982. Comparison of estimates of the predatory impact of ctenphores by two independent techniques. Mar. Biol. 68: 61-65.

Swanberg, N. 1974. The feeding behavior of Beroe ovata. Mar. Biol. 24: 69-76.

Swift, M. C. and A. Y Fedorenko. 1975. Some aspects of prey capture by Chaoborus larvae. Limnol. Oceanogr. 20(3):

418-426.

Theilacker, G. H. and R. Lasker. 1974. Laboratory studies of predation by euphausiid shrimps on fish larvae. In: J. H. S. Blaxter (ed.) The Early Life History of Fish. Springer-Verlag, Berl.

Tiselius, P. T. and W. T. Peterson. 1986. Life history and poplulation dynamics of the chaetognath Sagitta elegans in central Long Island Sound. J. Plankton Res. 8(1): 183-195.

Truesdale, F. M. and B. L. Andryszak. 1983. Occurrence and distribution of reptant decapod crustacean larvae in neritic Lousiana waters: July 1976. Contr. Mar. Sci. 26: 37-53.

Turner, J. T. 1982. The annual cycle of zooplankton in a Long Island estuary. Estuaries 5(4): 261-274.

Turner, J. T., S. F. Bruno, R. J. Larson, R. D. Staker and G. M. Sharma. 1983. Seasonality of plankton assemblages in a temperate estuary. Mar. Ecol. 4(1): 81-99.

Turner, J. T., P. A. Tester and W. F. Hettler. 1985. Zooplankton feeding ecology. Mar. Biol. 90: 1-8.

Van der Veer, H. W. and W. Oorthuysen. 1985. Abundance, growth and food demand of the scyphomedusa Aurelia aurita in the western Wadden Sea. Netherlands J. Sea Res. 19(1): 38-44.

Weinstein, M. P., S. L. Weiss, R. G. Hodson, and L. R. Gerry. 1980. Retention of three taxa of postlarval fishes in an intensively flushed tidal estuary, Cape

Fear river, North Carolina. Fish. Bull. 78(2): 419-436.

Wenner, E. L., D. M. Knott, R. F. Van Dolah and V. G. Burrell, Jr. 1983. Invertebrate communities associated with hard bottom habitats in the South Atlantic Bight. Estuar. Coast. Shelf Sci. 17: 143-158.

Westernhagen, H. von, H. Rosenthal, S. Kerr and G. Furstenberg. 1979. Factors influencing predation of Hyperoche medusarum (Hyperiida: Amphipoda) on larvae of the Pacific herring Clupea harengus pallasi. Mar. Biol. 51: 195-201.

Wood, L. and W. J. Hargis, Jr. 1971. Transport of bivalve larvae in a tidal estuary. In: Fourth European Marine Biological Symposium, D. J. Crisp (ed.) Cambridge University Press, NY, p. 29-44.

Yamashita, Y., D. Kitagawa and T. Aoyama. 1985. A field study of predation of the hyperiid amphipod Parathemisto japonica on larvae of the japanese sand eel Ammodytes personatus. Bull. Jap. Soc. Sci. Fish. 51(10): 1599-1607.